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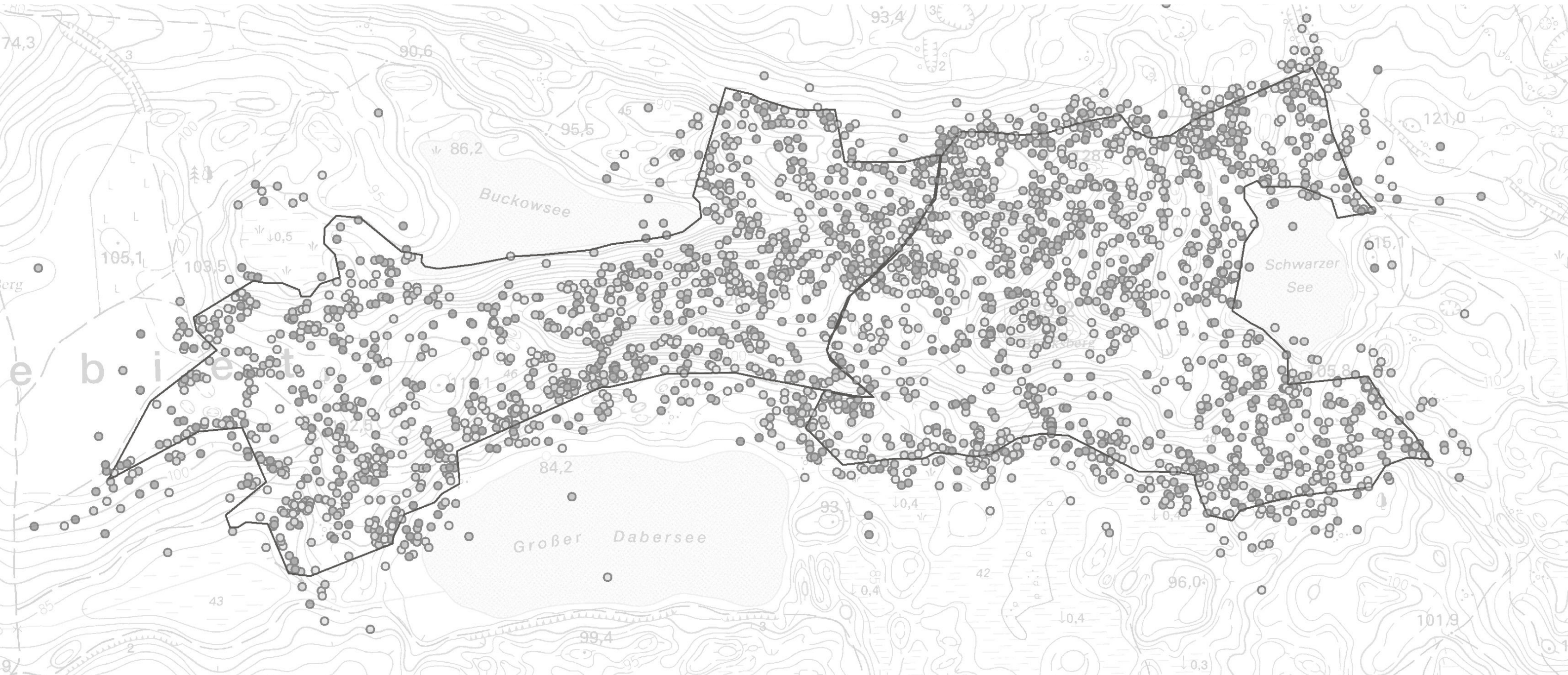

IMPACT OF NATURALNESS-PROMOTING BEECH FOREST MANAGEMENT ON THE FOREST STRUCTURE AND THE DIVERSITY OF BREEDING BIRDS

DISSERTATION
zur Erlangung des akademischen Grades
Doctor rerum naturalium (Dr. rer. nat.)

vorgelegt von
HEIKE BEGEHOLD

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ERKLÄRUNG DES PROVENDEN

Die Übereinstimmung dieses Exemplars mit dem Original der Dissertation zum Thema:

„Impact of naturalness-promoting beech forest management on the forest structure and the diversity of breeding birds“

wird hiermit bestätigt.

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PUBLICATIONS

Begehold H, Rzanny M, Flade M (2015) *Forest development phases as an integrating tool to describe habitat preferences of breeding birds in lowland beech forests.* Journal of Ornithology 156: 19–29. doi: 10.1007/s10336-014-1095-z

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Begehold H, Rzanny M, Flade M (2015) Erratum to: *Forest development phases as an integrating tool to describe habitat preferences of breeding birds in lowland beech forests.* Journal of Ornithology 156: 31–34. doi: 10.1007/s10336-014-1110-4

Begehold H, Rzanny M, Winter S (2016) *Patch patterns of lowland beech forests in a gradient of management Intensity.* Forest Ecology and Management 360: 69–79. doi: 10.1016/j.foreco.2015.10.021

Begehold H, Rzanny M, Winter S (submitted) *Impact of naturalness-promoting forest management on forest structure.* Annals of Forest Science

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Begehold H, Schumacher H (accepted) *Impact of naturalness-promoting management on breeding birds in lowland beech forests.* Vogelwelt

This manuscript does not appear.

SUPPLEMENTARY MATERIAL

A (Table)	Study sites, sizes, stand histories and Fagetum associations.
B (Table)	Breeding bird abundances in 20 lowland beech forest sites.
C (Table)	Significant differences of breeding bird abundances in comparison to the trend according to TRIM for the most common 34 breeding bird species.
D (Figure)	Flowchart to map FDPs
E (Figures)	Maps of FDPs in 22 lowland beech forest sites.

SUMMARY

Currently, existing European beech forests (*Fagus sylvatica* L.) are scarce and fragmented across vast parts of their potentially natural distribution. About 25 % of the global range of beech forests is located in Germany. Thus, Germany has a particular responsibility to integrate biodiversity conservation aspects into beech forest use.

In this thesis, the influence of naturalness-promoting management on forest structure and breeding birds was investigated – in comparison to management without a biodiversity focus (different management) and forests sites that have been unmanaged for different periods of time (recently: unmanaged for 14-32 years as of 2012, and long-term: unmanaged for 65 years or since at least 1900). With a total area of 714 ha, 22 study sites located in the northeastern part of Germany were studied. Forest structure was studied using forest development phases (FDPs), which divide the forest life cycle into different periods. FDPs are characterized by a defined combination of five structural parameters such as canopy cover, diameter at breast height, tree height, regeneration cover and deadwood amount. FDPs were mapped during the winters of 2012 and 2013 according to a dichotomic decision tree. Breeding bird abundances were determined in 19 study sites and each study site was mapped 10 times between March and July of the same years using a territory mapping method. FDP patterns such as proportions, patch sizes, distances between patches of the same FDP, evenness, FDP transition within a decade and transition diversity, as well as bird abundances and development of bird densities within a decade were analyzed.

Study sites under naturalness-promoting management differ clearly from differently managed sites and they are comparable or develop similarly to (long-term) unmanaged stands regarding FDP patterns. This also applies for the composition of the breeding bird community and the development of breeding bird species within a decade. The effect of naturalness-promoting management within the last decade is strong as evidenced by: significant decreases in FDP patches in size, the development of FDP richness towards a complete set; the comparability of transition proportion and transition diversity with long-term unmanaged sites (for former gaps, regeneration phase, early-, mid- and late optimum phase as well as disintegration phase); the higher total abundances of all breeding birds as compared with differently managed and recently unmanaged sites; and the highest number of increasing bird species amongst all management types. Further, the occurrence of breeding birds is linked to FDPs. On the one hand, the breeding bird community has a strong preference for FDPs of later-stages such as the terminal and disintegration phases. On the other hand, every bird species has its own set of preferred and avoided FDPs and every FDP has several bird species preferring it. Thus, a complete set of all FDPs at small scale is necessary for the habitat requirements of birds inhabiting beech forests.

In conclusion, 1) the positive impact of naturalness-promoting management on forest biodiversity is already detectable after a decade and 2) FDPs are a suitable indicator can be used as an innovative indicator for monitoring the impact of forest management on biodiversity.

INTRODUCTION

Nowadays, existing European beech forests (*Fagus sylvatica* L.) are threatened and fragmented across wide parts of their global range (e.g. Brunet et al. 2010). More precisely, the potential distribution of lowland beech forests extends in a narrow zone from northern France and southern Great Britain to the northern part of Germany, Denmark and southern Sweden and further to northern Poland (Bohn and Weber 2000, Bolte et al. 2007). Germany hosts the core area of global European beech forests, representing 25 % of this forest type's potential global range.

The primary aims of global and European conventions such as the Convention on Biological Diversity (CBD 1992), the Habitats Directive (92/43/EEC) and the biodiversity strategy of the Commission of the European Communities (2003) are the protection and sustainable use of forest resources and conservation of their biological diversity. These aims have been implemented into the respective national strategies of the ratifying countries. To monitor and evaluate the development of biodiversity and landscape quality across different landscape types, a survey of 59 selected bird species (performance indicators) has been established (for Germany: Bundesregierung 2002; Statistisches Bundesamt 2010).

The ecology of birds is, at least Europe-wide, well-known and because birds are the best studied taxon (Sudfeldt et al. 2010), it is possible to compare various studies. Further, birds rapidly colonize new and suitable habitats and they are sensitive to disturbances and changes in the use of natural resources (thereby functioning as biological indicators). In addition, bird abundances are connected to the vegetation structure, so many species act as target species in terms of nature conservation and implementation of measures (Schumacher 2005, Brunet et al. 2010, Sudfeldt et al. 2010). Finally, they are easy to detect and to record as their calls and songs provide adequate evidence for their presence. On these grounds, birds are predestined for nature conservation assessments. For forests, 11 bird species have been specified as indicators for biodiversity and landscape quality in the German National Strategy on Biodiversity (BMU 2007) and the National Sustainability Strategy (Bundesregierung 2002).

For birds, detailed studies verify that preferred landscape types, including forest types, for breeding do exist (e.g. Anderson and Shugart 1974; Flade 1994, 1995; Gregory and Baillie 1998). Further, the importance of single structures, microhabitats or parameters such as deadwood amount, have been identified for the occurrence and breeding of certain forest bird species (e.g. Frank 2002; Hertel 2003; Wesołowski and Rowiński 2004; Marti 2007; Smith 2007; Bühler 2009) or entire bird communities (Martin 1998; Schumacher 2005; Regnery et al. 2013). However, there is a lack of knowledge regarding the specific habitat requirements of forest birds within one forest type.

Many studies deal with the impacts of forest management on biodiversity, e.g. lower or different species richness and a less diverse and less complex forest structure in comparison to the natural reference (e.g. overview Paillet et al. 2010; Winter et al. 2005; Rosenvald and Lõhmus 2008). Thus, combining biodiversity conservation and the best use of forest resources is a goal that is repeatedly pursued by modern forestry (Flade et al. 2004; Winter et al. 2005, 2013; Kraus and Krumm 2013). In order to maintain forest biodiversity, integrative forest management requires the achievement of a near-natural stand structure in managed forests (e.g. Christensen and Emborg 1996; Suchan and Baritz 2001; Flade et al. 2004; Winter et al. 2005; Lindenmayer et al. 2006; Rosenvald and Lõhmus 2008; Kraus and Krumm 2013). Thereby, naturalness is an essential aspect for nature conservation and the preservation of global biodiversity (Reif and Walentowski 2008; Winter 2012). A high naturalness in managed forests is the only way to achieve high level forest biodiversity conservation (Winter et al. 2013).

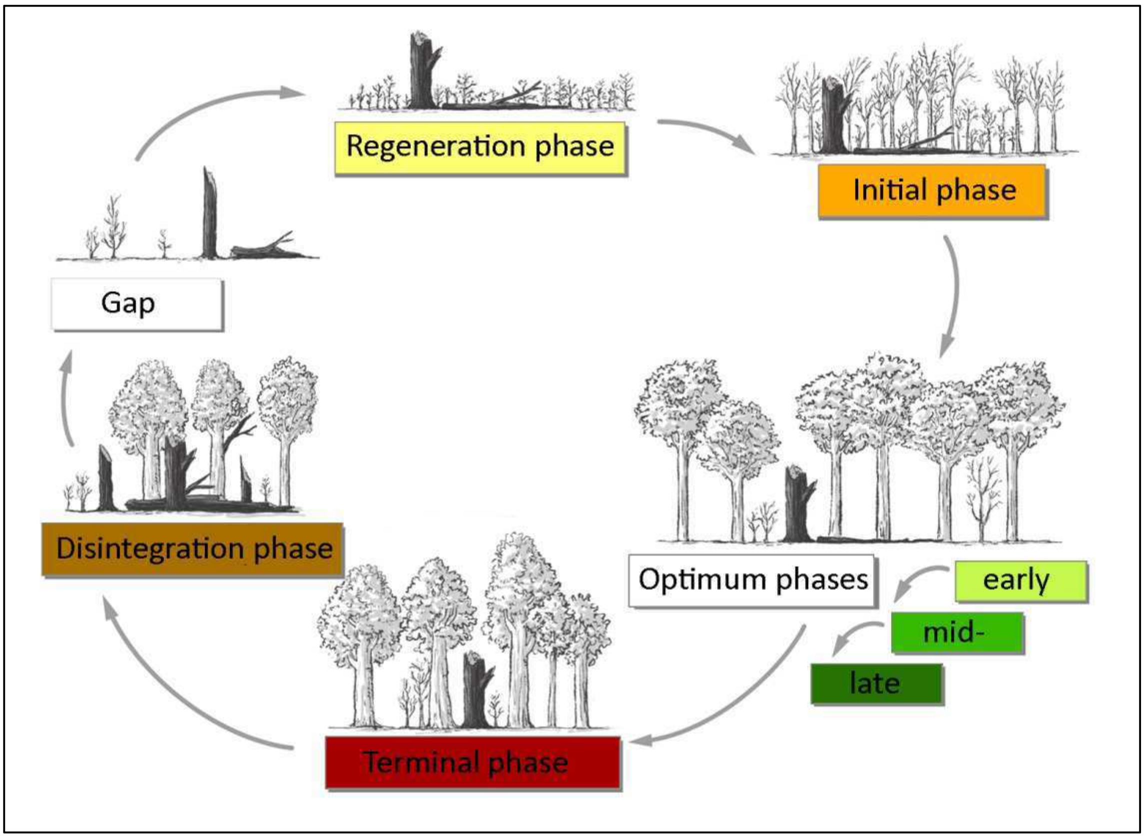

Fig. 1 FDPs as periods of the forest life cycle, simplified model for beech forests. The optimum phases differ in terms of tree dimensions (for information on the parameters defining the different FDPs see Begehold et al. 2016: Table 3). Figure modified according to Begehold et al. (2015a, b).

Forest development phases (FDPs) divide the forest life cycle into certain periods (Fig. 1). The natural structure of beech forests dominated by *Fagus sylvatica* is characterized by a fine-scaled mosaic of patches representing different FDPs (e.g. Watt 1947; Mueller-Dombois and Ellenberg 1974; Oldemann 1990; Remmert 1991; Korpel 1995; Bobiec et al. 2000; Emborg et al. 2000; Winter 2005; Král et al. 2010; Winter and Brambach 2011). Each FDP is defined by a particular set of structural forest stand parameters, such as diameter at breast height (DBH), canopy cover, tree height, deadwood amount and regeneration cover (e.g. Tabaku 2000). So, the total stand area is divided into a number of FDP patches, each running through cyclic succession processes corresponding temporal and spatial life cycle dynamics. These cycles are desynchronized among different patches (Wissel 1992). The spatial distribution of FDPs is a key aspect of habitat characteristics and therewith also of inhabiting species, the migration of individuals, populations or communities (Townsend et al. 2000).

As forest biodiversity is strongly connected to the forest life cycle and the presence of particular FDPs (Müller et al. 2005; Schumacher 2005; Winter et al. 2005; Winter and Möller 2008; Michel and Winter 2009; Winter and Brambach 2011), knowledge about the spatial distribution and texture of FDPs in managed beech forests – and comparisons between these and unmanaged beech forests – is important for maintaining the biological diversity. Further, the relation between FDPs and a suitable species group as breeding birds underlines the importance of FDPs for monitoring assessment. In this thesis, study sites managed with a naturalness-promoting focus have been compared with study sites without this management focus and unmanaged sites in order to analyze and evaluate the impact – within a decade – of a changed harvesting regime with regards to FDP patterns and breeding birds. In Europe, management impact on beech forest biodiversity has been studied (e.g. overview Brunet et al. 2010), but the effect of a changed harvesting regime in beech forests within a defined time period is missing.

Recent studies reveal that 1.9 % of the total woodland area in Germany is covered by forests with natural forest development (Engel et al. 2016); only 2 % of these is older than 200 years and only approx. 4 % was assessed as near-natural (on the basis of accordance of the main tree species and two mixed tree species with the potential natural vegetation). In Germany, beech forests have been reduced to approx. 8 % of their original area. Only a small proportion of the remaining beech forests is older than 160 years and only 0.2 % of the potential natural beech forest area is not subjected to any forest use (BfN 2008). These regions represent biodiversity hotspots, but they are often isolated and their area is insufficient to preserve the typical biodiversity of beech forests. So, biodiversity conservation aspects have to be incorporated into forest use (Winter et al. 2003; Kraus and Krumm 2013). Two research and development projects were carried out in the periods 1999-2002 and 2012-2014 in northeastern Germany to generate, specify and evaluate management criteria for naturalness-promoting forest management (Table 1).

In this context, the aim of this dissertation was to characterize

(1) the influence of naturalness-promoting management on the forest structure, especially FDP patterns, and the breeding bird composition in comparison to differently managed and unmanaged forest sites;
(2) the development of the forest structure and the breeding bird community within a decade; and
(3) the relationship between breeding birds and the stand structure with respect to particular FDPs.

METHODS

Study area

The study area consisted of 22 lowland beech forest sites in northeastern Germany (Fig. 2), located in the federal states of Brandenburg and Mecklenburg-Vorpommern. Eleven study sites were managed, of which seven were managed under a naturalness-promoting focus (Table 1) within the last decade and four were differently managed (without this focus). Eight sites were recently unmanaged (for 14-32 years as of 2012), of which two sites where former shelterwood loggings. One site was unmanaged for more than 65 years and two for more than 100 years (three long-term unmanaged sites). For further explanations on study sites see Supplementary Material A and Begehold et al. (2016: section 2.1).

Table 1 Silviculture concept for naturalness-promoting management (selection of measures affecting FDP structure) sourced from Begehold et al. (2016). For further explanations see Winter et al. (2003) and Flade et al. (2004).

1.	Silvicultural methods that result in simple and largely homogeneous stand structures, such as shelterwood logging and clearcuts, are not applied. Management units are smaller than one hectare to allow for a heterogeneous stand structure. Gaps are welcome and not filled by planted regeneration. The forest is, or will be, multilayered and diversely structured.
2.	Five old trees per hectare (> 40 cm DBH) are marked as habitat trees and allowed to develop microhabitats (Winter and Möller 2008) with natural ageing processes.
3.	A deadwood amount of at least 30 m^3 per hectare of standing and lying deadwood is provided in different dimensions (in nature conservation areas of 50 m^3 per hectare).
4.	Natural structures with habitat functions such as trees with broken crowns or broken trunks, trunks with lightning scars, trunk cavities, or bark pockets are preserved. At least 10 of 20 different microhabitat types as defined by Winter and Möller (2008) are present per hectare.
5.	The cutting threshold (trunk target dimension) should be at least 65 cm DBH. Trees should be present with trunk diameters which are successively greater than 65cm and moving towards those characteristic of very old habitat trees.
6.	Natural beech regeneration is used allowing for a near-natural mixture of indigenous tree species of around 15 %.
7.	A permanent system of skid trails (with a distance of at least 40 m) is determined, marked and maintained.
8.	Artificial drainage systems are removed and the natural water regime is restored. Mires and wetlands are maintained within the forest.

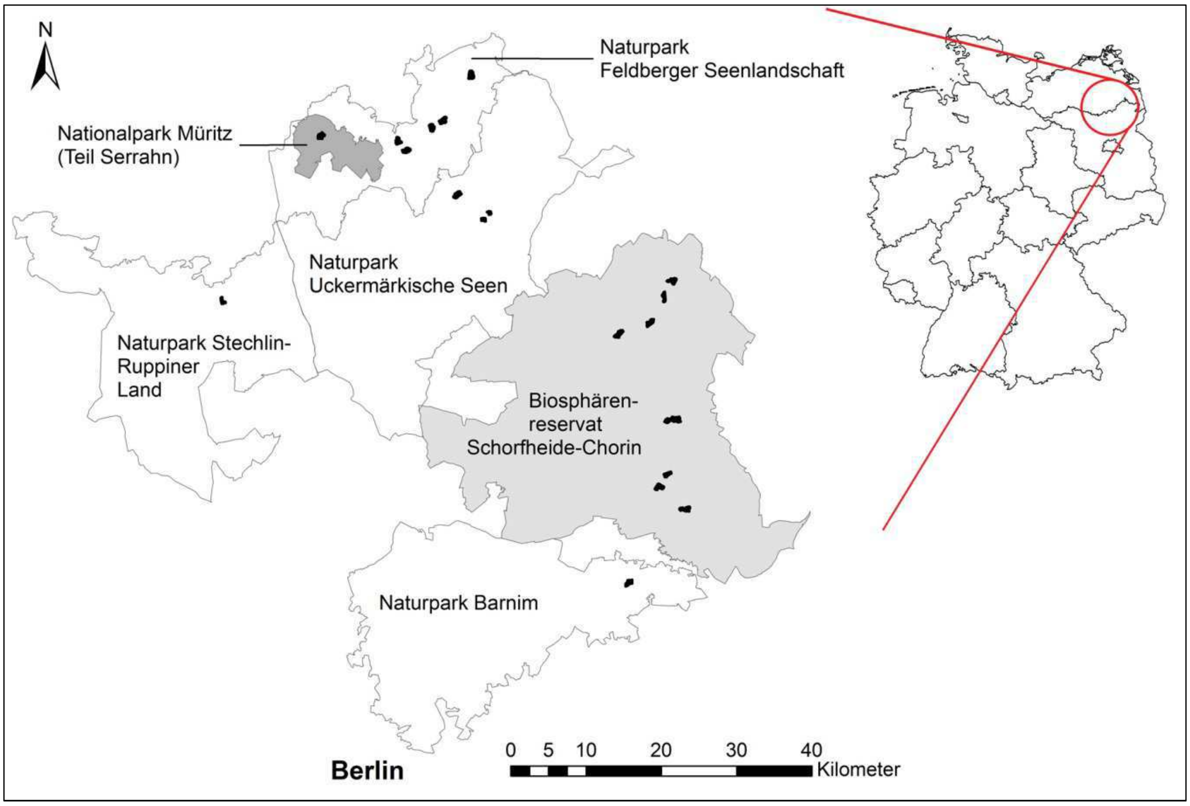

Fig. 2 Locations of the 22 study sites, all situated in large protected areas, in northeastern Germany (on the right hand, with borders of the federal states). White: Nature parks, light grey: Schorfheide-Chorin Biosphere Reserve, dark grey: Müritz National Park. Figure sourced from Begehold et al. (2016).

Mapping of forest development phases

In all study sites, forest development phases were recorded during the winters of 2011/12 and 2012/13 (see Supplementary Material D and E). FDP patches with a minimum size of 196 m^2 were determined according to a dichotomic decision tree developed by Tabaku (2000) and modified by Winter (2005: 28; Winter and Brambach 2011: Fig. 4 and Begehold et al. 2016: Table 3) with the expression of the following variables: more or less than 30 % canopy cover, DBH_{max}, tree $height_{max}$, more or less than 50 % regeneration cover and more or less than 30 % of standing and lying deadwood in relation to the total stock volume (for further explanations see Begehold et al. 2016: section 2.2). FDPs were mapped in the field and entered on a topographical map (1:3,000). In total, 714.3 ha were mapped. For nine study sites, FDP maps from 2002 (Winter 2005) as result of the first research and development project were used to analyze the development of FDP patterns within a decade. One of these nine sites could only be used for the time series analysis of FDP proportions due to a poor match of the forest- and topographical maps during the two recording periods.

Bird mapping

In 19 study sites, breeding birds were mapped in 2012 or 2013. In each study site, the presence of breeding birds was recorded 10 times between mid-March and mid-July. The breeding bird survey was carried out using an extended territory mapping method (Flade 1994; Südbeck et al. 2005). Additionally, where possible, every bird individual was assigned to the FDP in which it was present during the first registration of each record. For further explanations see Begehold et al. (2015a: method section). To analyze the development of the bird abundances, data from records from the period 1998-2002 in 18 of the same study sites, mapped by Schumacher (2005), and a trend index (TRIM) for the development of the breeding bird abundances in the Schorfheide-Chorin Biosphere Reserve, were used.

Data entry and analyses

FDP maps were digitalized as polygon shape files in the ESRI geographical information system (ArcGis 9.3.1, ESRI, Redlands, CA). Patch number, patch sizes and proportions of the single FDPs were calculated with the Arc Toolbox. Changes in FDP identity within the ten-year time period were determined by comparing the FDP patch identity from 2002 with that of 2012/13. They were then defined as FDP persistence (the same FDP in 2002 and 2012/13) or transition (different FDPs in 2002 and 2012/13). Distances between patches of the same FDP were calculated in each study site (ArcInfo Workstation v. 9.3) based on the minimum distance between patch edges.

A model of natural FDP distribution was created and, with reference to this, the duration of each FDP was estimated according to growth tables, literature and studies in northeastern Germany. For further explanations see Begehold et al. (2016: section 2.3 and Fig. 2)

The Index of Aggregation (Clark and Evans 1954) was calculated to determine the spatial patch distribution between patches of the same FDP. A value of $R = 0$ indicates a maximal aggregation of the patches. The degree of aggregation decreases with an increasing value of R until a random patch distribution is reached ($R = 1$). Values of $R > 1$ indicate a regular patch distribution (see also Begehold et al. 2016).

Pielou's evenness index (Pielou 1966) was used to calculate the structural evenness according to FDP proportions. It quantifies the equality of different FDP proportions within a study site. Therewith, the differences between FDP structure in different study sites and management types were compared and also contrasted with the evenness of the structure modelled for a natural FDP distribution (see also Begehold et al. 2016).

The Shannon Index (Shannon 1948) was used to calculate the diversity of different FDPs into which one FDP converts (FDP transition from 2002 to 2012/13; see also Begehold et al., submitted).

Bird registrations were entered as point shape files in ArcGis. To determine breeding territories, minimum convex polygons were calculated (Hawth's analyzing tools, v. 3.27).

The Jacobs selectivity index (Jacobs 1974) was used to determine breeding bird species' preference for, or avoidance of, for single FDPs. This varies between +1 and -1, where positive values show preference for a certain FDP and negative values indicate avoidance (see also Begehold et al. 2015a). Jacobs indices were calculated for each bird species on the basis of single registrations and breeding territories.

The DDA TRIM index (Trends and Indices for Monitoring Data; Pannekoek and van Strien 1998), as trend index for the development of the breeding bird abundances based on the German Common Bird Census (DDA 2016), was used to determine significant differences in the single bird abundances between the 1998-2002 (Schumacher 2005) and 2012/13 records based on the general trend in the Schorfheide-Chorin Biosphere Reserve. The index includes all influence factors on the population density of breeding birds; e.g. weather parameters such as precipitation and temperature (cold winters), forest tree fruiting, insect availability, vegetation growth, population dynamics of small mammals as well as the impact of the wintering site conditions. The expected value a_{exp} of species abundance a was calculated for each bird species and per study site using the following formula:

$$a_{exp} = \frac{a_{first\ record} \cdot TRIM_{second\ record}}{TRIM_{first\ record}}$$

Using the 95% confidence interval for a_{exp}, the significant difference d of the recorded abundance $a_{second\ record}$ was determined to be decreasing (-1), displaying no difference (0) or increasing (1) in comparison to the trend identified by the TRIM index. In this way, the sum of all d values of the study sites belonging to one management type was built. Therewith, a species within a management type is shown to be mainly increasing (positive sum), mainly decreasing (negative sum) or not developing differently (sum is zero) in comparison to the trend outlined by the TRIM index. The data base for the TRIM index includes all landscape types.

To illustrate the relation between and the similarity of the study sites, Principal Correspondence Analysis (PCA) as well as non-metric multidimensional scaling (NMDS) was applied to:

- patch sizes and proportions of the single FDPs (see also Begehold et al. 2016),
- mean minimum distances between patches of the same FDP (see also Begehold et al. 2016),
- breeding bird abundances (Begehold and Schumacher, accepted)

Procrustes superimposition (Gower 1971) was used to determine the degree of concordance between:

- the composition of the breeding bird community and FDP composition (mean patch size, proportions or patch numbers of the single FDPs, see also Begehold et al. 2015a),
- FDP compositions (proportions) in 2002 and 2012/13 (see also Begehold et al., submitted).

95% confidence intervals were calculated to make comparisons across study sites and management types and with reference values.

All calculations and graphics were computed in R (R Core Team 2012) using the packages vegan (Oksanen et al. 2013) and compositions (vd Boogaart et al. 2013) or Microsoft Excel.

MAIN RESULTS

Impact of naturalness-promoting management on FDP patterns

Significant differences between management types are revealed by comparing structural parameters such as FDP patch sizes (Fig. 3) and FDP proportions (Supplementary Material E; Begehold et al. 2016: Fig. 3, Appendices 2 and 3). Although still significantly different, the value for evenness – characterized by **FDP proportion** and richness of the single FDPs – in sites under naturalness-promoting management is closest to that of the long-term unmanaged sites and to the model value of the potential natural FDP proportions (see Begehold et al. 2016: Fig. 4). Under naturalness-promoting management, evenness is similar within study sites and differs significantly from differently managed study sites. These two management types also differ significantly with regards to mean FDP patch size (Fig. 3). According to this parameter, there are also significant differences between recently and long-term unmanaged sites.

Generally (as found for all management types), **patch sizes** of gaps (median of 310 m^2), regeneration phase (400 m^2), terminal (460 m^2) and disintegration phase (350 m^2) are smaller than for the other FDPs (initial phase: 490 m^2, early optimum phase: 540 m^2, mid-optimum phase: 745 m^2, late optimum phase: 570 m^2; see also Begehold et al. 2016: Appendix 3; Begehold et al., submitted: Table 2 and Fig. 5).

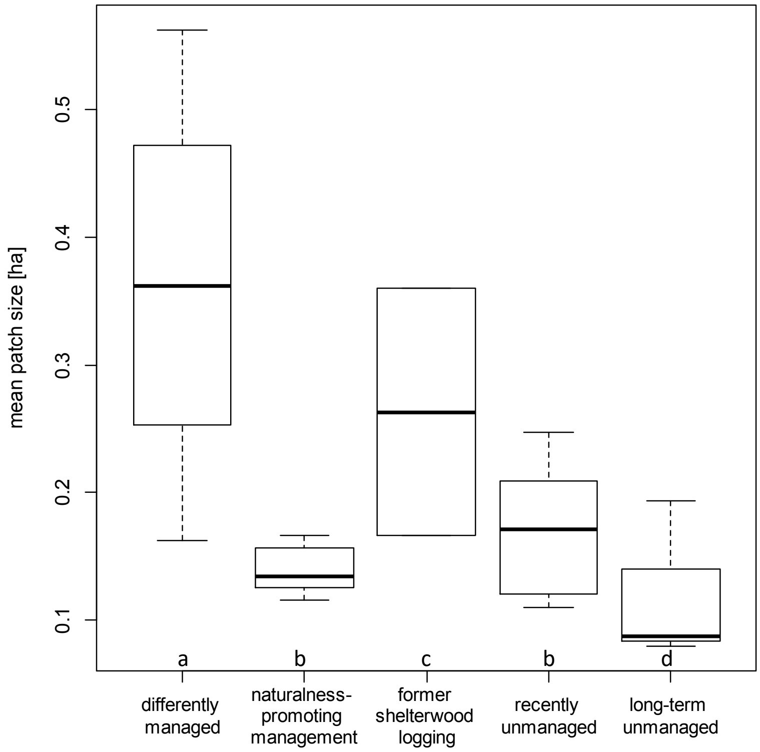

Fig. 3 Boxplot of the mean patch sizes in 22 lowland beech forest sites; Four differently managed sites (551 patches, 167.2 ha), seven sites under naturalness-promoting management (2,089 patches, 269.5 ha), two former shelterwood logging sites (196 patches, 28.5 ha), six recently unmanaged (1,022 patches, 167.6 ha) and three long-term unmanaged sites (806 patches, 81.6 ha). Significant differences between management types are indicated by different lowercase letters, calculated with the help of 95% confidence intervals.

The **spatial distribution of patches** of the same FDP differs between management types: Under naturalness-promoting management, regeneration phase and late optimum phase patches are (the most) aggregated, which differs significantly from other management types (see Begehold et al. 2016: Fig. 6 and Appendix 5). Further, in long-term unmanaged sites, early optimum phase as well as disintegration phase patches are the most aggregated compared to the other management types, and mid-optimum phase patches are less aggregated.

Impact of different management types on the breeding bird community

The **total abundances** of all breeding bird species differs clearly across management types (Figs. 4: right, and 5). In study sites under naturalness-promoting management, the total abundance is higher than in differently managed study sites, higher than in sites unmanaged for 14 years (including the two former shelterwood logging sites) and higher than in the two Grumsin sites k2 and k3 (unmanaged for 23 years). In sites under naturalness-promoting management, total abundance is comparable to two of the long-term unmanaged sites, while the long-term unmanaged site r3 shows by far the highest total abundance (Fig. 5: top). The **species number** differs across all study sites (with 23-34 species) and these differences do not correlate with management types. In three sites under naturalness-promoting management, the highest species number of 34 was found. The two former shelterwood logging sites w4 and w6 are apart with much lower species numbers and species abundances. These statements also apply to the wood inhabiting species (Fig. 5: bottom and Supplementary Material B).

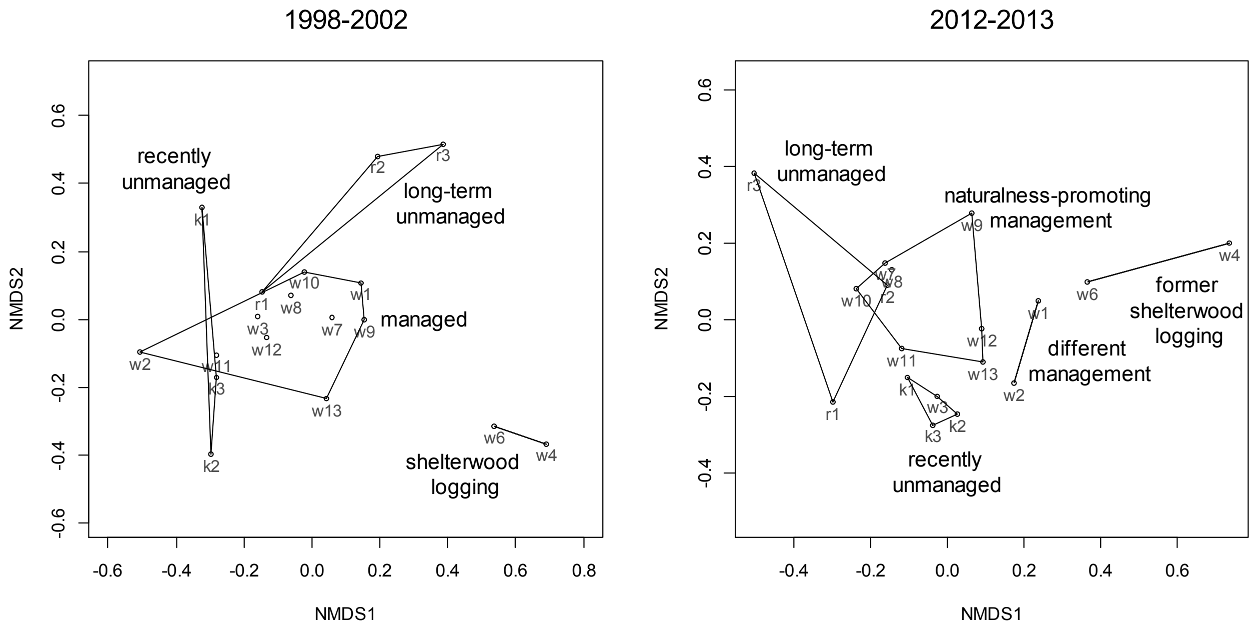

Fig. 4 Graphical display of the NMDS ordination of 18 study sites (based on Jaccard Dissimilarity) according to the breeding bird abundances in 1998-2002 (left) and 2012/13 (right). For further explanations on study sites see Supplementary Material A. Figure according to Begehold and Schumacher (accepted).

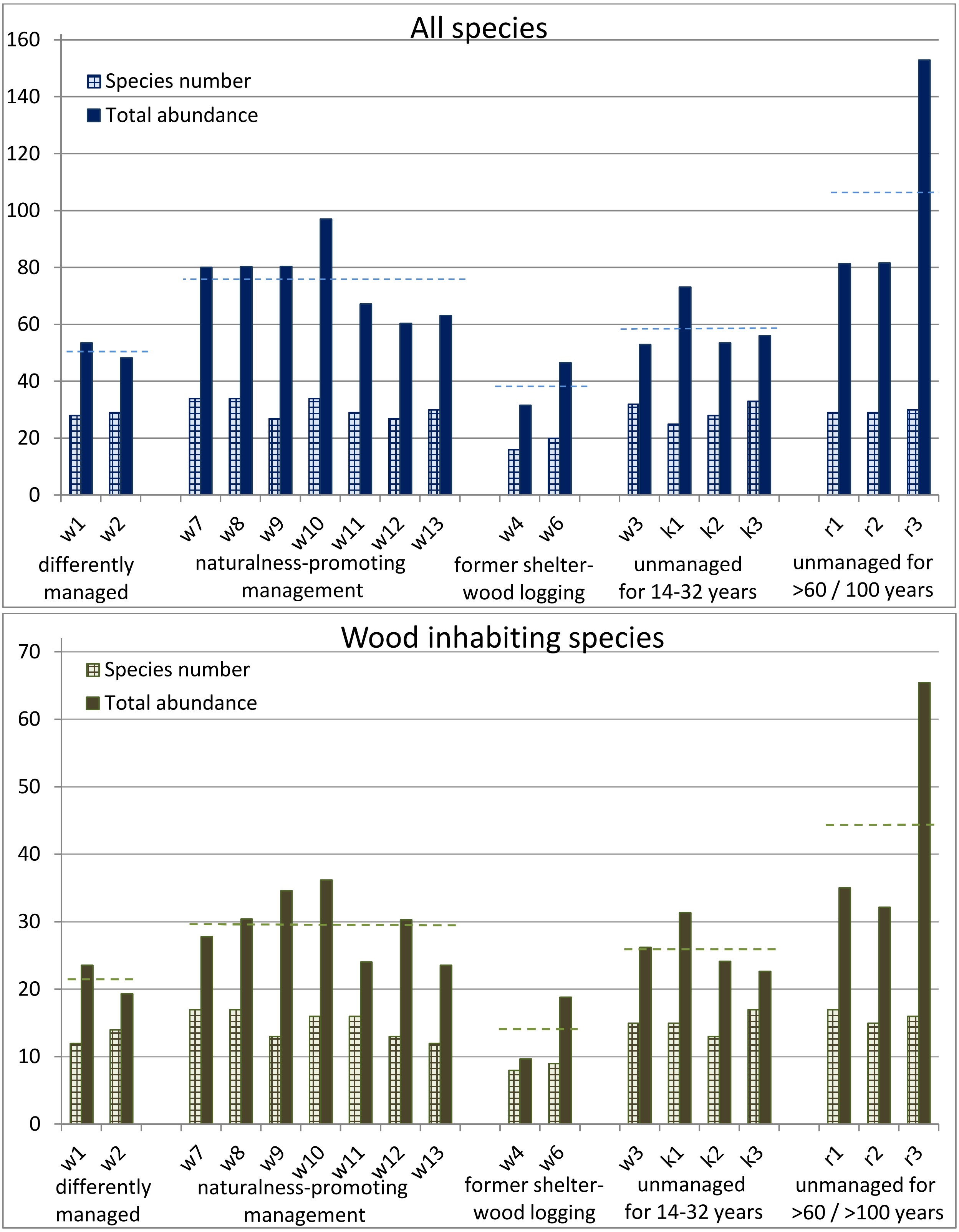

Fig. 5 Species number and total abundances of all (top) and wood inhabiting bird species (bottom) in five management types based on the records in 2012/13 with mean total abundances (dashed lines). For further explanations on study sites see Supplementary Material A. Figure modified according to Begehold and Schumacher (accepted).

Changes in forest structure within a decade in different management types

In comparison to unmanaged sites, the greatest proportion of the stand area under naturalness-promoting management developed into another FDP during the last decade (on average, 59 % of the area changed FDP, compared with 29 % in recently unmanaged and 31 % in long-term unmanaged sites). Nevertheless, the **proportion of the area changes** regarding single FDPs was similar to recently unmanaged sites (see Begehold et al., submitted: Fig. 2a). FDP composition for each study site was rather similar in both recording periods (Procrustes correlation $r = 0.8764$, Begehold et al., submitted: Fig. 2b).

The proportion of FDP that changed into another FDP within the last decade (**FDP transition**), as well as the Shannon diversity of the FDPs that converted into other FDPs (**transition diversity**) was different for single FDPs and across management types (Begehold et al., submitted: Figs. 3 and 4). Under naturalness-promoting management, transition proportion and transition diversity was comparable to long-term unmanaged sites for former gaps, regeneration phase, the optimum phases and disintegration phase (Fig. 6). Gaps and regeneration phase patches underwent a high transition proportion in all management types.

Across all management types, **mean patch size** decreased between 2002 and 2012/2013 (Begehold et al., submitted: Table 2), although this decrease was only significant for naturalness-promoting management ($p < 0.001$, Wilcoxon Rank Sum test). However, median patch sizes of single FDPs developed differently across the management types within the decade (see Begehold et al., submitted: Fig. 5). For further explanations see Begehold et al. (submitted).

There are clear differences to the differently managed stand without nature conservation focus; however, it is not possible to generalise on the basis of a single site. Nevertheless, the transformation of gaps, early and late optimum phases into the mid-optimum phase is most explicit in this differently managed site and a large percentage of the mid-optimum phase persisted (Fig. 6e). Only 10% of the area of former mid-optimum phase patches changed into a subsequent FDP although the proportion of trees close to the FDP threshold of 60 cm diameter at breast height differentiating the mid- and late optimum phases was comparable to the other management types (for naturalness-promoting management the turnover proportion was 55 %). Further, only a small percentage of late optimum phase patches persisted, whereas under naturalness-promoting management, persistence and transition diversity was significantly higher (Fig. 6 f).

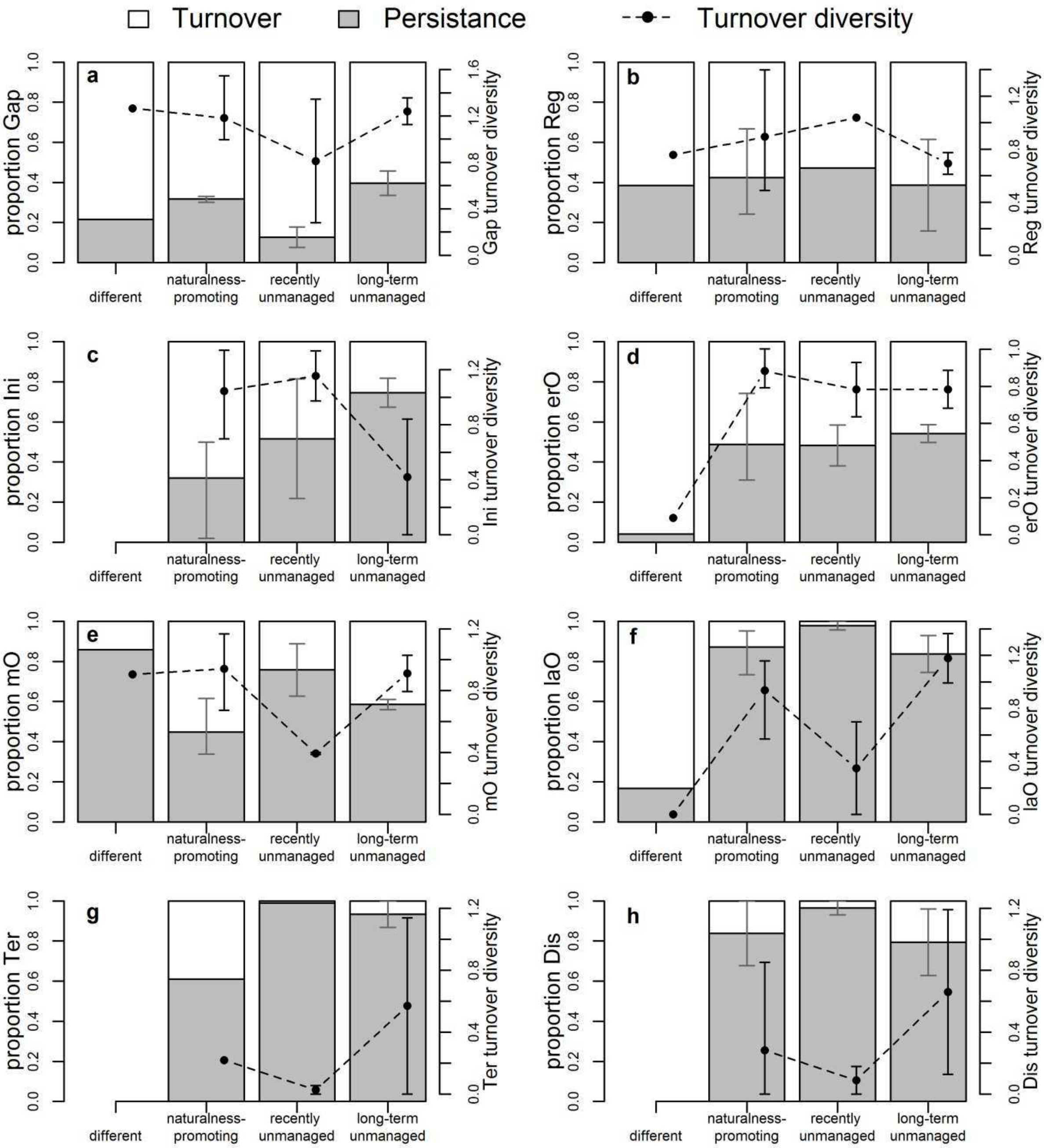

Fig. 6 Proportion of persistence (the percentage of patch area that was assigned to the same FDP as 10 years ago; grey bars) and transition (turnover = the percentage of patch area that transformed into a different FDP compared to the earlier recording; white bars) as well as transition diversity (Shannon diversity of the patches that transformed into a different FDP; points) of FDPs over ten years in managed and unmanaged beech forest sites. Error bars represent ranges across study sites. Reg = regeneration phase, Ini = initial phase, erO = early, mO = mid- and laO = late optimum phase, Ter = terminal phase and Dis = disintegration phase. Figure modified according to Begehold et al. (submitted). Here, a separate analysis of the recently unmanaged former shelterwood and the other recently unmanaged site was not useful due to the low sample size.

Trends of breeding birds within a decade in a management gradient

Management types differ in terms of the abundances of all breeding bird species within the study sites. Based on the records in 2012/13, the first axis of the NMDS clearly reflects a gradient that can be seen as a management gradient or as a gradient of ageing structures of the sites (Fig. 4). Study sites under naturalness-promoting management are demarcated from the differently managed sites and are similar and more related to the long-term unmanaged sites a decade after the first recording. The recently unmanaged study sites show similarities with each other and can be differentiated from the managed sites. The former shelterwood logging sites w4 and w6 are still clearly different from the other management types (Fig. 4, 5 and Begehold and Schumacher, accepted).

Under naturalness-promoting management, the number of increasing species in comparison to the trend shown by the TRIM index is highest when comparing all management types (Fig. 7); 27 of the most common 33 breeding bird species show a stronger positive tendency than the **development indicated by the TRIM index** (followed by recently unmanaged (23) and long-term unmanaged (19) sites), three develop in line with the index and only three species have a lower trend than indicated by the TRIM index (Lesser Spotted Woodpecker, Coal Tit and Common Starling). Amongst the different management types, this is the lowest number of species with a non-positive trend. In contrast, in differently managed and in former shelterwood logging sites, the number of species with a positive trend in comparison to the TRIM index was only 14 and 10, respectively (Fig. 7 and Begehold and Schumacher, accepted).

The differences between management sites are also underlined by the development of the **breeding guilds** (Table 2). In sites under naturalness-promoting management, all free breeders and ground breeders as well as the majority of hole and niche breeders show a significant positive trend according to the TRIM index. A similar pattern is present in recently unmanaged sites.

Table 2 Significant differences in comparison to the trend shown by the TRIM index for the breeding guilds of the most common 34 breeding bird species (with a presence in at least nine study sites during the first (1998-2002) and/or the second record in 2012/13). **+** significant positive trend, **–** significant negative trend, **0** no difference.

Management / Guild	Differently managed			Naturalness-promoting management			(Former) shelterwood logging			Recently unmanaged			Long-term unmanaged		
Development	**+**	**0**	**–**	**+**	**0**	**–**	**+**	**0**	**–**	**+**	**0**	**–**	**+**	**0**	**–**
Free breeders (n=11 species)	2	8	1	11	0	0	4	5	2	10	1	0	7	3	1
Hole breeders (n=15 species)	6	8	1	9	3	3	4	8	3	5	8	2	6	5	4
Niche breeders (n=5 species)	1	3	1	4	1	0	1	3	1	4	1	0	3	2	0
Ground breeders (n=3 species)	1	1	1	3	0	0	1	1	1	3	0	0	2	1	0

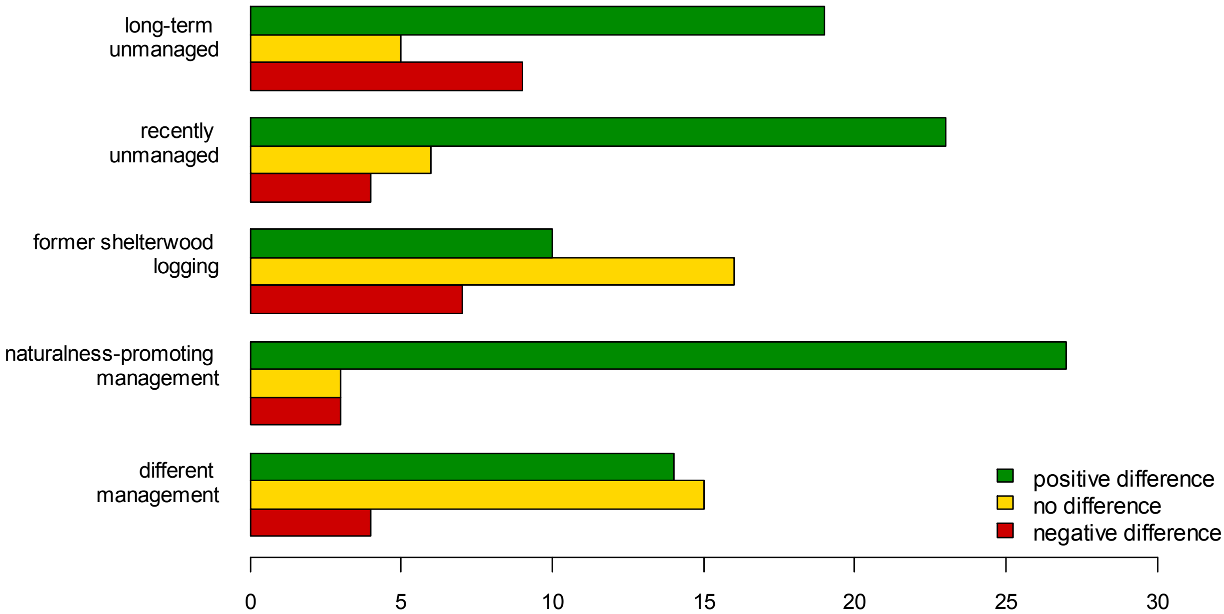

Fig. 7 Significant differences in comparison to the trend indicated by the TRIM index for the most common 33 breeding bird species with a presence in at least nine study sites at the first (1998-2002) and/or the second record (2012/13). Figure modified according to Begehold and Schumacher (accepted).

Correlation between breeding birds and FDPs

For breeding birds, a high **correlation to FDPs** was detected: Procrustes superimposition confirmed that the proportion, patch sizes and patch numbers of FDPs are strongly connected to the breeding bird composition (Procrustes residuals of 0.618, 0.606, 0.551, see also Begehold et al. 2015b: Fig. 5). Further, the terminal and disintegration phases are strongly preferred by the breeding bird community of the 24 most common species (Fig. 8) as well as by all nesting guilds (see Begehold et al. 2015b: Fig. 3) as demonstrated by Jacobs indices close to a value of 1. In addition, every bird species has its specific profile of preferred and avoided FDPs, and each FDP is designated as a preferred habitat by (a) certain species (Table 3; Begehold et al. 2015b: Fig. 4). For further and detailed explanations see Begehold et al. (2015a).

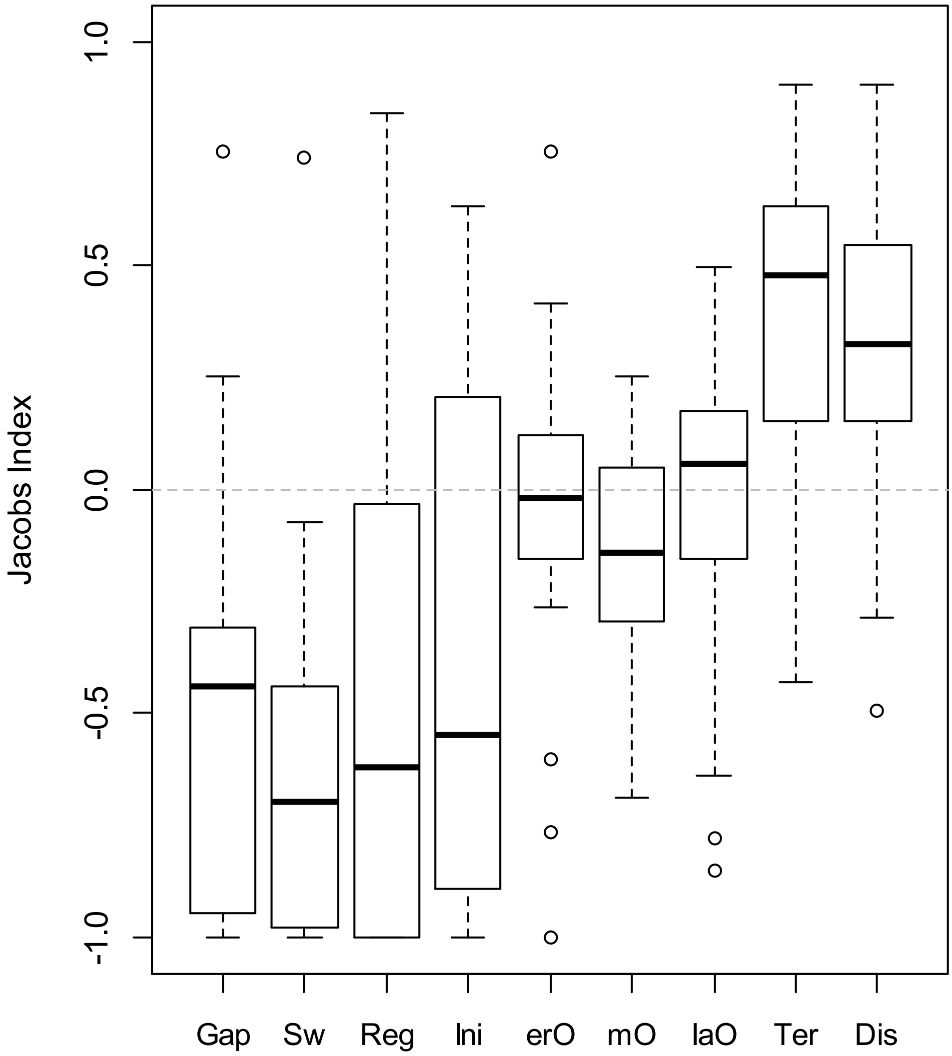

Fig. 8 Boxplot of Jacobs indices of the most common 24 breeding bird species (with at least 70 registrations) for FDPs in lowland beech forests. Positive values indicate preference for, and negative values indicate avoidance of, the respective FDP. A value of zero (dashed line) indicates neither preference nor avoidance. For FDP abbreviations see Fig. 6.

Table 3 Mean Jacobs indices for FDPs across study sites for the most common breeding bird species based on single registration data. Values that appear in bold refer to significant differences from zero, i.e. significant preference (green) or avoidance (red) of the respective FDP. For FDP abbreviations see Fig. 6.

Species names		FDP								
Scientific name	Common name	Gap	Sw	Reg	Ini	erO	mO	laO	Ter	Dis
Dendrocopos major	Great Spotted Woodpecker	**-0,90**	**-0,85**	**-0,68**	**-0,87**	-0,07	0,10	0,00	0,04	0,16
Erithacus rubecula	European Robin	**-0,71**	**-0,65**	0,22	**0,27**	-0,01	**-0,33**	**-0,25**	**-0,25**	0,35
Turdus merula	Common Blackbird	-0,04	**-0,81**	**0,58**	0,17	**-0,49**	**-0,24**	**-0,33**	**-0,18**	-0,12
Sylvia atricapilla	Eurasian Blackcap	**-0,42**	**-0,88**	**0,77**	**0,28**	-0,26	**-0,59**	**-0,71**	**-0,53**	-0,22
Phylloscopus sibilatrix	Wood Warbler	-1,00	-1,00	-0,42	**0,61**	**0,74**	**-0,71**	**-0,88**	**-0,83**	-0,43
Troglodytes troglodytes	Eurasian Wren	**0,60**	**0,76**	-0,28	**-0,48**	-0,08	**-0,78**	**-0,76**	**-0,49**	**0,69**
Parus major	Great Tit	**-0,68**	**-0,76**	0,15	**0,23**	0,04	-0,28	-0,03	0,13	0,08
Parus caerulus	Eurasian Blue Tit	**-0,68**	**-0,84**	-0,10	0,02	-0,02	-0,28	0,05	**0,34**	0,03
Sitta europaea	Eurasian Nuthatch	-1,00	-1,00	**-0,92**	**-0,74**	**-0,33**	0,16	0,02	0,22	0,07
Certhia familiaris	Eurasian Treecreeper	-1,00	**-0,93**	-1,00	**-0,89**	-0,03	-0,12	0,12	-0,02	0,13
Fringilla coelebs	Common Chaffinch	**-0,94**	**-0,95**	**-0,81**	**-0,60**	0,27	-0,07	0,05	**0,31**	-0,06
Coccothraustes coccothraustes	Hawfinch	**-0,84**	-1,00	-1,00	-1,00	**-0,67**	-0,02	**0,39**	-0,12	-0,38

DISCUSSION

The particular importance of naturalness-promoting management for FDP patterns and breeding birds

The results of this study with regards to (changing) FDP proportions (Begehold et al., submitted: Fig. 2) and mean FDP patch sizes (Fig. 3; Begehold et al. 2016: Fig. 3), FDP evenness (Begehold et al. 2016: Fig. 4), mean minimum distances between patches of the same FDP (Begehold et al. 2016: Fig. 5) and FDP transition (Fig. 6; Begehold et al., submitted: Figs. 3 and 4) underline a varying impact of the different management types on FDP structure. In this study, FDP patterns follow a clear management gradient for all these parameters; study sites under naturalness-promoting management differ clearly from sites under different management but are comparable to, or develop similarly to, (long-term) unmanaged stands. This also applies for the composition of the breeding bird community (Figs. 4 and 5) and the non-negative development of almost all breeding bird species within a decade (Fig. 7).

For this study and with the given conditions of the studied beech forest stands (Supplementary Material A), there is a higher diversity of FDPs and mean patch sizes are smaller after a decade of naturalness-promoting management compared to differently managed sites. The disintegration phase as an important component of forest biodiversity (e.g. Möller 2005; Müller et al. 2005; Winter and Möller 2008) accumulated within the last decade in these study sites. Further, they show a high transition proportion from the mid-optimum phase (which is a dominant FDP in our managed forests) as well as high transition diversity. These results show that FDP structure in managed sites with a naturalness-promoting silviculture concept (Table 1) can create a structure that approaches that found in unmanaged stands. Moreover, the changed to a silviculture concept that promotes naturalness is rapidly detectable. In addition, this concept is a practicable and feasible measure with nature conservation criteria confirming the integration of nature conservation aspects into management directives (e.g. Kraus and Krumm 2013). For further detailed classifications and comparisons with literature see Begehold et al. (2016) and Begehold et al. (submitted).

The positive effect of naturalness-promoting management is confirmed in relation to the abundances of almost all breeding bird species in this study. This effect might be different in other beech stands with another “starting point”: In younger stands where old trees, microhabitats and deadwood are less frequent, a naturalness-promoting management might show a different result. However, some species such as the Red-breasted Flycatcher with its high habitat requirements were also documented in sites under naturalness-promoting management which contrasts with results from Boncina (2000).

Reasons for the positive trends of the breeding bird abundances in sites under naturalness-promoting management are the increase in the tree age and corresponding increase in DBH (hole breeders, free breeders, e.g. Bütler et al. 2014), microhabitats and amount of deadwood (hole breeders, niche breeders, ground breeders; e.g. Winter and Möller 2008, Brunet et al. 2010), as well as the growth of the young tree regeneration to a layer of shelter, breeding and feeding habitat (ground breeders, some free breeders). As the positive trend of forest species is also the result of a significant increase in settlements in contrast to stagnation or (significant) decrease in forests (Flade and Schwarz 2004; Data from the German Common Bird Census; e.g. Great Spotted Woodpecker, Green Woodpecker, Common Wood-Pigeon, Eurasian Jay, Short-toed Treecreeper, Common Treecreeper, Eurasian Wren, Eurasian Nuthatch, Great Tit, Long-tailed Tit, Marsh Tit, Coal Tit, European Robin, Firecrest), the positive trend in the studied beech forest sites might be more powerful than demonstrated here.

The significant role of FDPs, inter alia for breeding birds

Forest biodiversity is strongly connected to the forest life cycle and the presence of certain FDPs (e.g. Winter and Möller 2008). The results of this thesis prove three facts:

(1) On the one hand, the specific role of the terminal and disintegration phases has been demonstrated for the breeding birds community (Fig. 8; Begehold et al. 2015b: Fig. 3; Schumacher 2005), as is also confirmed by studies for several other taxa; i.e. for saproxylic beetles (Möller 2005, Müller et al. 2005), bats (Meschede 2000) or for bryophytes and lichens, where some rare species and indicator species for ecological continuity are associated with large tree diameters and shady conditions with a moist forest interior (Friedel at al. 2006), which is typical for the terminal phase.

(2) On the other hand, other FDPs are preferred by single breeding bird species, meaning that the occurrence of (nearly) all FDPs is important for the varying habitat requirements of the bird species (Table 3; Begehold et al. 2015b: Fig. 4). This has also been proven for other taxa, which prefer FDPs other than the terminal or disintegration phases, such as gaps for herbaceous plants (Winter 2005) or growing stages such as the regeneration and initial phases for centipedes (Grgič and Kos 2005).

(3) Further, the stand structure, characterized by FDP composition and mean FDP patch sizes, is linked to the inhabiting breeding bird community (Begehold et al. 2015b: Fig. 5), meaning that appropriate FDP proportions as well as a reasonable texture of FDPs are required (Haila et al. 1996; Heikkinen et al. 2004). The presence of many FDPs at small scale also plays an important role for ectomycorrhizal fungi (Read 1987, Keizer and Arnolds 1994). A small-scale mosaic (Haila at al. 1996, Flade et al. 2004) and the proportions of different FDPs (Haila et al. 1989) is important for the habitat heterogeneity within the forest and therefore for forest biodiversity (Mitchell et al. 2006, Hewson et al. 2011). Regarding the temporal component, the permanent presence of all FDPs within a stand to maintain the structural and habitat continuity is of crucial value. For further detailed classifications and comparisons to literature see Begehold et al. (2015a).

FDPs as indicator for describing forest dynamics

FDPs combine different structural key parameters such as DBH and tree height, canopy cover, regeneration cover and deadwood amount, which in turn integrate forest habitat conditions, e.g. light conditions, microclimate, deadwood structures and microhabitats. All of them influence food availability, shelter or reproduction sites and therefore the spatial distribution of diverse taxa. The demarcation of FDPs is an important analytical approach to detect changes in forest structure; to illustrate the natural structural dynamics; to describe and quantify the patchiness and FDP proportions; and in particular to picture and monitor the complex habitat conditions of forests. For these reasons, FDPs represent a suitable indicator to describe forest conditions and dynamics.

Mapping of FDP is relatively fast, cheap and easy to interpret – in comparison to other monitoring assessments as, for instance, a full structural inventory of plots by measuring or remote sensing methods and a following construction of FDP maps with the help of programmed models (e.g. an artificial neural network as used by Král et al. 2014). In dense beech forests, the record of DBH, regeneration or (standing) deadwood is still not accurately possible by remote sensing methods (Heurich et al. 2004, Heurich 2008, Polewski et al. 2015). Moreover, I had to use the methods of the first research and development project to keep consistency for comparing the two data sets. Remote sensing methods improved during the last decade, but were not fundable during the research projects.

However, the monitoring of FDPs should be integrated into nature conservation monitoring assessments such as NATURA 2000 and used to verify the conservation status of FFH sites (92/43/EEC), for instance by defining a minimum number of different FDP per a defined unit area or by mapping FDP, at least at plot level. The recording of FDPs is a useful measure to evaluate the effect of (naturalness-promoting) forest management, and to compare the development to documented changes of forest structure and biodiversity in unmanaged sites.

These results should be used for implementation of nationwide binding criteria for the management of beech forests: to promote (1) FDPs such as terminal and disintegration phases (up to a proportion of at least 5 %) and (2) a small-scale mosaic of almost all FDPs (e.g. at least five different FPDs per hectare, see also Winter et al. 2015).

CONCLUSIONS

Positive effects of naturalness-promoting management were already detectable after one decade. FDP richness increased and was combined with decreasing FDP patch sizes which unexpectedly approached forest conditions that are characteristic of recently unmanaged forests.

The rapidly detectable changes in the forest texture were described using the combination of FDP proportions and patch sizes of the single FDPs. Thus, these two indicators are suitable for, and proposed as means of picturing and monitoring habitat conditions of forest inhabiting (bird) species. Given that FDPs have until now been seen as strata or age structures rather than aggregated ecosystematic units, their ecological meaning promises to elucidate (through monitoring) the complex connection between forest structure and forest biodiversity.

However, the applicability of FDP mapping is limited in relation to tropical forest ecosystems, due to single tree cycles, as well as to some boreal forests with disturbances that are too coarse in scale such as forest fires that create homogenous and even-aged stands. Nevertheless, the results of this thesis might be applicable at least for other deciduous forests in Europe; at least with an adapted mapping scheme integrating the number of tree species. Further investigations should be carried out to explore the extent to which coniferous forests show comparable patterns. Moreover, FDPs should be used for the determination of a favorable conservation status as required by the EU Habitats directive for Natura 2000 sites. FDP mapping will not compensate or replace other indicators such as the recording of deadwood but it provides a meaningful picture of habitat conditions.

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ORIGINAL ARTICLE

Forest development phases as an integrating tool to describe habitat preferences of breeding birds in lowland beech forests

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Abstract Land management causes changes in forest structure and thus influences the composition and abundance of communities of forest-inhabiting bird species. However, it is unclear how these changes translate into local habitat suitability for certain bird species given that detailed knowledge on habitat use by forest bird species is still scarce. We have analyzed the habitat preferences of 37 breeding bird species in 19 lowland beech forests, each with an average size of 40 ha. We used Jacobs habitat selection index to quantify preference or avoidance of certain forest developmental phases (fdp). Fdp divide the forest life cycle into different periods, each characterized by a certain combination of habitat parameters (canopy cover, tree dimension, deadwood amount, regeneration cover), thereby integrating several age-specific structural properties. We found that fdp representing the last third of the forest life cycle were significantly preferred by most of the bird species. Of the 37 bird species analyzed, 19 showed the highest preference for the terminal phase or the disintegration phase; this was especially true for hole breeders, semi-hole breeders, ground breeders and beech forest indicator species. Moreover, each bird species showed a characteristic profile of preferred and avoided fdp. Some bird species, such as several free breeders, also preferred younger fdp, such as gaps or regeneration phases. Further, mean fdp patch size turned out to be a strong predictor of bird community composition. Our study confirms that most bird species show a strong preference for later fdp, such as the terminal phase and disintegration phase. However, the simultaneous availability of a mixture of different fdp on local scales meets the habitat preferences of most species and promotes biodiversity of breeding bird communities in lowland beech forests.

Keywords Habitat use · Jacobs index · Breeding bird community · Nesting guilds · Forest developmental stages · Forest structure

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Zusammenfassung

Waldentwicklungsphasen als ein integrierendes Werkzeug zur Beschreibung von Habitatpräferenzen von Brutvögeln innerhalb von Tieflandbuchenwäldern

Die Bewirtschaftung von Wäldern bewirkt verschiedenste Veränderungen in deren Struktur und beeinflusst dadurch die Zusammensetzung und Abundanz der dort vorkommenden Arten. Dabei ist jedoch der Einfluss dieser Veränderungen auf die lokale Habitatstruktur noch unklar und es mangelt an Kenntnissen zu detaillierter Habitatnutzung durch verschiedene Brutvogelarten. Wir haben Habitatpräferenzen von 37 Brutvogelarten in 19 jeweils ca. 40 Hektar großen Buchenwaldgebieten untersucht. Mit Hilfe des Jacobs Index wurde das artspezifische Präferenz- und Meidungsverhalten für bestimmte Waldentwicklungsphasen (WEP) bestimmt. WEP unterteilen den Lebenszyklus des Waldes in verschiedene Abschnitte, die jeweils durch eine bestimmte Kombination von Habitatparametern wie Kronenschlussgrad, Baumdimension, Totholzanteil und Deckungsgrad der Verjüngung charakterisiert sind, wobei alterstypische, strukturelle Eigenschaften integriert werden. Unsere Ergebnisse zeigen, dass die WEP im letzten Drittels des Lebenszyklus eines Waldes von den meisten Vogelarten bevorzugt werden. 19 von 37 Arten präferieren die Terminal- oder Zerfallsphase am stärksten, insbesondere Höhlenbrüter, Halbhöhlenbrüter, Bodenbrüter sowie die Buchenwald-Leitarten. Darüber hinaus zeigt jede Vogelart ein spezifisches Profil, das sich aus präferierten und gemiedenen WEP zusammensetzt und sich zwischen den Arten deutlich unterscheidet. Einige Arten, z.B. Freibrüter, bevorzugen auch jüngere WEP wie beispielsweise Lücken oder Verjüngungsphasen. Desweiteren erwies sich die mittlere WEP-Patchgröße als bedeutender Faktor für die Artenzusammensetzung der Brutvogelgemeinschaft eines Waldbestandes. Unsere Untersuchung unterstreicht, dass die meisten Brutvögel spätere WEP bevorzugen. Dennoch deckt sich das gleichzeitige Vorkommen *aller* WEP in einer kleinteiligen mosaikähnlichen Struktur mit den Habitatpräferenzen der Vögel und begünstigt die Biodiversität von Brutvogelgemeinschaften in Tiefland-Buchenwäldern.

Introduction

Existing beech forests (*Fagus sylvatica*) are scarce and fragmented across vast parts of their global range. More specifically, lowland beech forests are potentially distributed in a narrow zone that extends from northern France and southern Great Britain to the northern part of Germany, Denmark and southern Sweden and further to northern Poland (Bohn and Weber 2000). The core area of global copper beech forests occurs on German territory, representing 25 % of its global range. With the aim of effective quality control management, modern forest is consistently searching for the best ways to integrate biodiversity conservation with the best use of forest resources (Flade et al. 2004; Winter et al. 2005, 2013).

The primary aims of the Convention on Biological Diversity (the 'Biodiversity Convention'), which entered into force for signatory countries in December 1993, are the conservation of biodiversity and a sustainable use of forest resources. Countries ratifying the Convention have implemented these aims into their respective national strategies. Indicator species were chosen to monitor and evaluate the actual progress and the development of biodiversity across different landscape types (for Germany: Bundesregierung 2002; Statistisches Bundesamt 2010). For forests, 11 bird species were chosen as indicator species, of which seven breed in the beech forest sites of our study.

Bird species abundance is decreasing across most landscape types (Sekercioğlu et al. 2004; Dierschke et al. 2011, p. 52), including woodlands (Robinson et al. 1995; Gregory et al. 2007). In Germany, "out of 52 forest bird species monitored by the German Common Birds Survey, much more species were in decline (24 species) than increasing (10 species)" during the period between 1991 and 2013 (Flade 2013). Included in many of the possible factors affecting bird species abundance are the effects of climate change on the condition of the wintering and stopover sites (Lemoine et al. 2007a; Schaefer et al. 2008; Jenouvrier 2013), land use (Lemoine et al. 2007b), habitat fragmentation and habitat loss (Lynch and Whigham 1984; Andrén 1994; Robinson et al. 1995; Trzcinski et al. 1999; Angelstam et al. 2004). In order to improve habitat conditions and thereby simultaneously improve an important part of ecosystem functionality, it is necessary to know how birds use their habitats in detail and which parts and structures are most important.

The results of detailed studies prove that preferred landscape types for breeding do actually exist (Anderson and Shugart 1974; Flade 1994, 1995; Gregory and Baillie 1998). Also, the importance of single structures, microhabitats or parameters such as deadwood amount, have been clarified for particular forest bird species, such as the European Nuthatch (*Sitta europaea*) (Wesołowski and Rowiński 2004), Wood Warbler (*Phylloscopus sibilatrix*) (Marti 2007), White-backed Woodpecker (*Dendrocopos leucotos*) (Frank 2002; Bühler 2009), woodpeckers (Hertel 2003; Smith 2007) or entire bird communities (Martin 1998; Schumacher 2005; Regnery et al. 2013). There is, however, a need to investigate the specific complex habitat requirements of forest birds within forests that can be applied operationally (for example, mapping in the field, habitat suitability assessments, calculation of potential habitat area size and quality). There is also a lack of tools for describing and surveying the habitat quality of forest patches in detail. Different forms and qualities of one forest type can be identified by the characterization of forest development phases (fdp), which divide a forest's life cycle into certain periods (Fig. 1; Table 1) while combining structural forest stand parameters (Table 1). For beech forests, Tabaku (2000) developed a method to investigate fdp in natural beech forests. Winter (2005) modified this method for lowland beech forests and adapted it to a much easier usage in the field. In our study, each phase is defined by a particular set of structural forest stand parameters, such as canopy cover, diameter at breast height (dbh), tree height, deadwood amount and regeneration cover. Therefore, the relative proportions of fdp embedded in the mosaic of the whole forest stand provide integrated, important information on forest structure and condition. As forest biodiversity is strongly associated with the forest life cycle and the occurrence of certain fdp (Knapp and Jeschke

Fig. 1 Simplified model of the forest life cycle in beech forests. Early, medium and late optimum phases differ only in tree dimensions; for details see Table 1

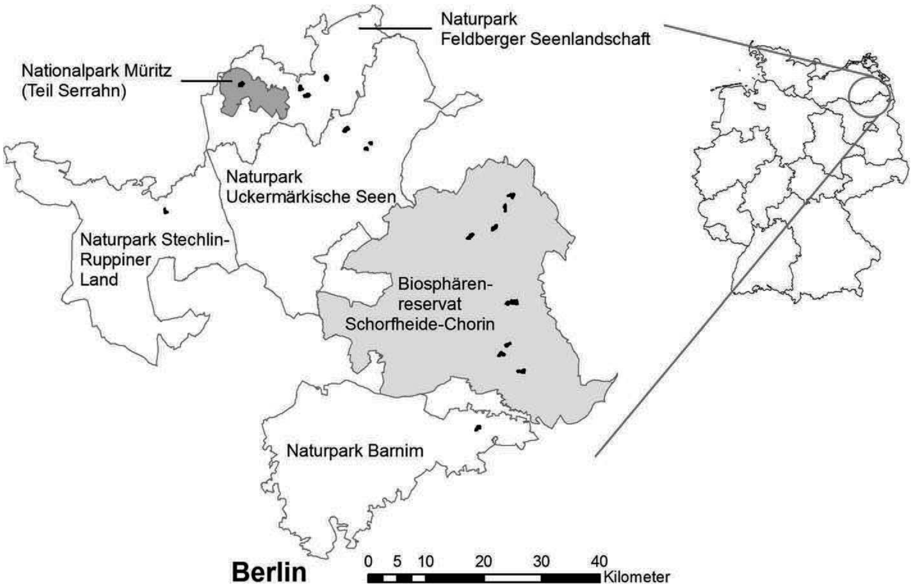


Table 1 Description of different forest development phases according to habitat parameters[a]

Fdp[b]	Parameters[c]
Gap	Canopy cover <30 %, regeneration cover <50 %, any amount of deadwood
Regeneration phase	Canopy cover <30 %, regeneration cover >50 %, any amount of deadwood
Initial phase	Canopy cover >30 %, dbh <20 cm, any amount of deadwood
Early optimum phase	Canopy cover >30 %, 20 cm < dbh_{max} ≤40 cm, amount of deadwood <30 %
Medium optimum phase	Canopy cover >30 %, 40 cm < dbh_{max} ≤60 cm, amount of deadwood <30 %
Late optimum phase	Canopy cover >30 %, dbh_{max} >60 cm, amount of deadwood <30 %
Terminal phase	Canopy cover >30 %, dbh_{max} >60 cm, height >85 % of potential height (= 45 m), amount of deadwood <30 %
Disintegration phase	Canopy cover >30 %, dbh >20 cm, amount of deadwood >30 %

Fdp, Forest development phases; dbh, diameter at breast height (1.3 m from ground); dbh_{max}, largest dbh within patch; deadwood, proportion of standing and lying deadwood in the total stock volume within the patch

[a] According to Winter (2005) and Winter and Brambach (2011)

[b] The minimum size of an fdp patch was 14 × 14 m

[c] Canopy cover refers to canopy cover of all trees with a dbh >7 cm. Regeneration includes all tree individuals after the seedlings stage and with dbh <7 cm

1991; Winter and Brambach 2011), specification of the habitat use by forest birds helps to complete the habitat requirements of forest-inhabiting species.

Forest development phases are rarely studied with respect to habitat use by birds. The results of earlier studies suggest that forest birds prefer the terminal phase (Winter et al. 2002, 2003; Flade et al. 2004) and, like many saproxylic species (Möller 2005; Müller et al. 2005; Fichtner et al. 2014), the disintegration phase (Schumacher 2005; Winter et al. 2005). For broad-leaved woods, Ghadiri Khanaposhtani et al. (2012) showed that birds prefer either late or early successional stages.

Within the framework of the global responsibility of Germany to sustain copper beech forests, the aims of this study are:

1. To evaluate the preference and avoidance behavior of the breeding bird community in beech forest stands with respect to particular fdp;
2. To define specific profiles for selected species associated with different fdp;
3. Analyze the relationship between bird community and stand structure.

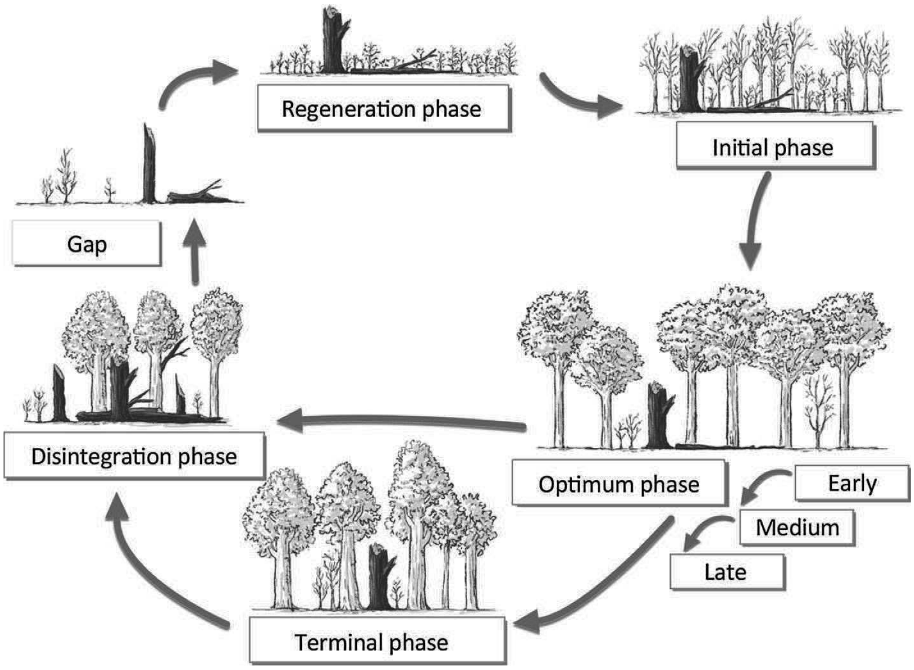
These data are essential to assess the importance of a more comprehensive consideration of fdp in managed forests to maintain beech forest biodiversity.

Methods

Study area

We investigated fdp and breeding bird assemblages in 19 lowland beech forest stands, of which ten were managed, four were unmanaged for a relatively short period of time (14–

Fig. 2 Locations of the 19 study sites and large protected areas (national park, biosphere reserve, nature parks) in north-eastern Germany. *White* Nature parks, *shading in light gray* Schorfheide-Chorin Biosphere Reserve, *shading in dark gray* Müritz National Park



32 years), two were former shelterwood logging stands and three were long-term unmanaged stands (one for >60 years and two near-natural stands unmanaged for >110 years). All study sites were mature stands and at least 120 years old (two of the reference stands are >300 years old). All stands belong ecologically to mixed *Fagetum* associations, with most sites belonging mainly to the *Galio odorati–Fagetum* association, and three belonging for the most part to the *Luzulo–Fagetum* association (Fischer 1995). The study sites are located in the north-eastern part of Germany, between 52.8 and 53.3°N and 13.0 and 13.9°E (Fig. 2). Soil conditions are rather similar within study sites with a sufficient supply of water and nutrients (Kopp and Schwanecke 1994). Due to the ground and terminal moraine characterization of the Late Pleistocene, the study site areas are characterized by pronounced inhomogeneous soils. Climate conditions are similar within the study stands (sub-continental, altitude varies between 43 and 130 m a.s.l., mean annual precipitation about 519−629 mm/year, mean annual temperature 8.4−8.9 °C (Deutscher Wetterdienst 2013). Most stands were about 40 (range 30.4−44.9) ha, with the exception of the two reference sites (13.6 and 24.9 ha, respectively), two sites which were only just recently unmanaged (12.3 and 20.1 ha, respectively) and the two former shelterwood logging sites (11.4 and 17.1 ha, respectively).

Habitat map with respective fdp

We mapped all of the study site areas and assigned each patch to a particular fdp (according to Tabaku 2000, as modified by Winter 2005). Fdp assignment was based on a dichotomous decision tree, in which fdp were distinguished by different parameters, such as canopy cover, regeneration, dbh, amount of lying and standing deadwood and tree height (see Fig. 3 in Winter and Brambach 2011; Table 1). Kettle holes formed by retreating glaciers ultimately became small swamps that represent typical elements of these forests; these were mapped additionally to the fdp. Fdp and swamps were determined directly in the field, with a minimum patch size of 14 m × 14 m, transferred according to their local position and extension as patches onto a topographical map (1:3,000) and demarcated from neighboring fdp patches by means of a GPS device and a fixed (marked) grid of circle study plots (100 × 200 m).

Bird mapping

The breeding bird survey was performed as an extended territory mapping method (Flade 1994; Südbeck et al. 2005). Each study site was visited ten times between mid-March and mid-July, and birds were recorded and mapped across the total study site area. For each visit, a new map was created (1:3,000), and the presence of birds together with the following attributes were recorded: species name, sex, age (adult or juvenile), behavior and interaction with other birds. The position of each bird was visibly or acoustically registered and assigned to a specific fdp when this assignment was unambiguous. In all other cases, the individual was still registered and the data was used to determine breeding bird territories. Following this procedure, we were ultimately able to count the number of records for each bird species within each fdp.

In order to determine breeding territories, we created species maps based on all single registrations of all the ten visits. All registrations originating from different visits and unequivocally representing different breeding pairs were assigned to a single breeding territory. Additionally, a singing male had to be present at least once within a species-specific period (Südbeck et al. 2005).

We used the minimum convex polygon method to digitalize breeding territories in the ESRI geographical information system (ArcGIS 9.3.1; ESRI, Redlands, CA) with Hawth's analysing tools (v3.27). Minimum convex polygons are accepted as a standard method for modeling species' ranges and are used to assess tendencies in occupied habitat (Burgman and Fox 2003). To study the use of fdp within the breeding territories, we calculated the proportion of different fdp per territory. Parts of breeding territories beyond the border of the study site were not included in the analyses, and only that part within the study site was taken into account. Additionally, only territories of three or more single registrations of the species were considered as a territory. Therefore, the abundance of breeding territories of some long-distance migratory bird species like the Red-breasted Flycatcher (*Ficedula parva*), which arrives comparatively late in May or June, might be underestimated in the our dataset. Abundances were calculated as number of territories per 10 ha.

Habitat use

To determine the use of fdp in beech forests by birds, we used Jacobs selectively index (Jacobs 1974), which varies between -1 and $+1$. Positive values indicate a preference for a certain habitat, while negative values indicate avoidance. The availability of each fdp (resource units) is represented by the relative fraction of the site area covered by each of the respective fdp. Fdp with a relative fraction of the site area of <0.5 % were excluded from the analysis (this occurred only rarely). Jacobs index was calculated for single registrations and for breeding territories. The proportion of fdp used for single registrations and for breeding territory area (used units), was determined and calculated for each bird species. For territory analysis, we used the fdp proportion across all territories and study sites. Territory sizes were rather similar within species. The Jacobs index was calculated for all species with at least 70 registrations across all study sites or at least 20 territories. For the mean across study sites, we considered only species occurring in at least seven study sites with at least 20 registrations per site. Differences between fdp used by all breeding bird species were tested using the Wilcoxon rank sum test. To account for multiple testing, p values were adjusted using Bonferroni corrections. 95 % confidence intervals for the means across study sites were calculated for Jacobs indices per species and fdp to test whether they differed significantly from zero, which would indicate that the fdp was used more or less often than would be expected based on the proportion of its availability.

Relationship of breeding bird communities and large-scaled stand structure

We used Procrustes superimposition (Gower 1971) to determine the degree of concordance between fdp composition and composition of the breeding bird community. Procrustes superimposition measures the degree of correspondence of two ordinations (Gower 1971)—one according to the abundance of all breeding bird species and the other according to one of three stand structure parameters, i.e. proportion, mean patch size and patch number per fdp. In order to achieve Procrustes superimposition, we calculated an non-metric multidimensional scaling (NMDS) ordination for the community composition dataset and for each of the fdp composition datasets. For fdp proportions we calculated NMDS ordination based on Aitchison dissimilarity to account for the compositional nature of these data. The remaining datasets were square root transformed to downweight the effect of abundant species or fdp. The NMDS for bird species abundances was based on Bray−Curtis dissimilarities. NMDS was performed with five axes and resulted in stress values of <0.05. Procrustes superimposition was followed by the subsequent permutation procedure PROTEST (Jackson 1995) with 9,999 permutations to estimate Procrustes correlation t and the statistical significance of the Procrustes fit. The different measures were compared based on their degree of concordance to the breeding bird abundances.

All calculations and graphics were computed in R (R Core Team 2012) using the package 'vegan' (Oksanen et al. 2013) and compositions (vd Boogaart et al. 2013).

Results

Habitat use based on single registrations

We used data from 26,995 registrations across all study sites, of which 11,654 could be assigned to one of eight fdp or swamps. For 37 breeding bird species, the number of registrations was ≥20 across all study sites ($n = 11{,}606$ registrations); 24 bird species were registered >70 times ($n = 11{,}234$). The number of species with positive Jacobs index increased towards the late fdp within the successional cycle (terminal and disintegration phase; Fig. 3). This trend is also reflected in all guilds: terminal and/or disintegration phase were significantly preferred by each guild (Table 2). Median Jacobs indices across all species for the disintegration phase and for the terminal phase were significantly greater than those for all other fdp

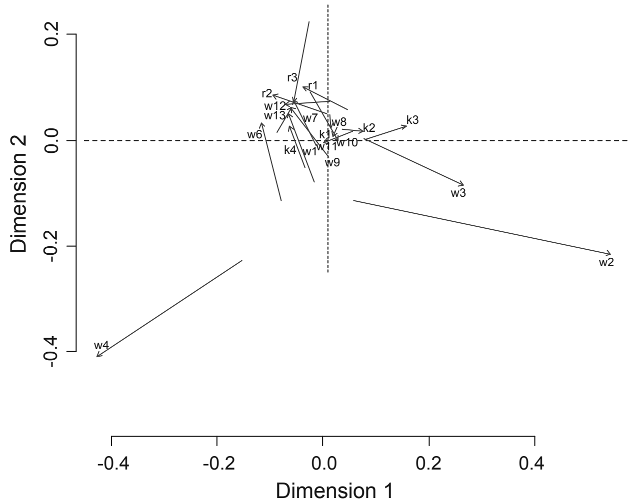


Fig. 3 Jacobs indices according to single registrations of breeding birds, ecological guilds (*yellow*) and among beech forest indicator species (*asterisk*; Flade 1994; Schumacher 2005). Included are 24 species each with more than 70 single registrations across all study sites. Species abbreviations are given as the EURING (European Union for Bird Ringing) code (*bottom of graph*)

($p < 0.01$; for late optimum phase compared to disintegration phase, $p = 0.036$; Table 2). Additionally, median Jacobs indices for the optimum phases did not differ significantly from each other, but they did differ from the fdp gap and swamp, which in turn were not significantly different from each other. The median Jacobs indices for regeneration (−0.64) and initial phase (−0.56) were much lower, but not significantly different from the optimum phases.

Habitat use based on breeding territories

Three or more registrations were made at 3,897 of the 4,050 breeding territories; these could be depicted as minimum convex polygons. Mean number of registrations per minimum convex polygon was 5 (± 1.8 standard deviation, SD). A territory could be calculated based on more than ten registrations if the two sexes were registered separately (e.g., for woodpeckers).

For 24 species, the total number of territories was >20 across all study sites (the same species with at least 70 single registrations). Jacobs indices for these bird species (and nesting guilds), based on territories, differed from those based on single registrations (Table 2), but tendencies (positive or negative Jacobs index values) were the same, except for swamps and the regeneration phase.

The disintegration phase was associated with significantly higher Jacobs indices compared to the early ($p = 0.033$) and medium optimum phases, respectively ($p = 0.039$). No significant differences were detected among the remaining fdp (Table 2). When testing for species with >50 territories (18 species), the medium optimum phase still differed significantly from the disintegration phase ($p = 0.002$) and, additionally, from the late optimum phase ($p = 0.046$).

Species-specific habitat preferences

For 12 common species, occurring in 7−18 study sites, we also calculated the mean Jacobs index across all study sites. We used these analyses to develop a species-specific

Table 2 Median Jacobs indices per fdp for 24 breeding bird species and all study sites, as well as significant preferences and avoidances to fdp by different nesting guilds, according to single registration data for species each with >70 registrations and according to territory areas for the same species each with >20 territories

Fdp	Single registration data				Territory area data			
	Median Jacobs index[a]	Median absolute deviation	Preference[b]	Avoidance[b]	Median Jacobs index[a]	Median absolute deviation	Preference[b]	Avoidance[b]
Gap	−0.4373 a	±0.5988		G, F, H, FS	−0.0207 a, b	±0.1227		
Swamp	−0.6169 a	±0.4174		G, F, H, FS	0.0115 a, b	±0.2126		FS
Regeneration phase	−0.6186 a, b	±0.5655		SH, H, FS	0.0281 a, b	±0.1169	F	
Initial phase	−0.5489 a, b	±0.6688	G	SH, H, FS	−0.0806 a, b	±0.2683	G	SH, H
Early optimum phase	−0.0168 b	±0.2033			−0.0411 a	±0.1186		F
Medium optimum phase	−0.1417 b	±0.2408		G, H	−0.0385 a	±0.0794		G, H, FS
Late optimum phase	0.0585 b	±0.2661			0.0297 a, b	±0.0480	H	
Terminal phase	0.4780 c	±0.4014	F, SH, H, FS		0.0262 a, b	±0.2835	H, FS	
Disintegration phase	0.3255 c	±0.3094	G, SH, H, FS		0.0980 b	±0.1577	G, H, FS	

G, Ground breeders; F, free breeders; SH, semi-hole breeders; H, hole breeders; FS, flagship species

[a] Significant differences between used fdp are indicated followed by different lowercase letters following the median Jacobs index

[b] Significant preference/avoidance was tested as differences to a Jacobs index value of 0 by calculating a 95 % confidence interval

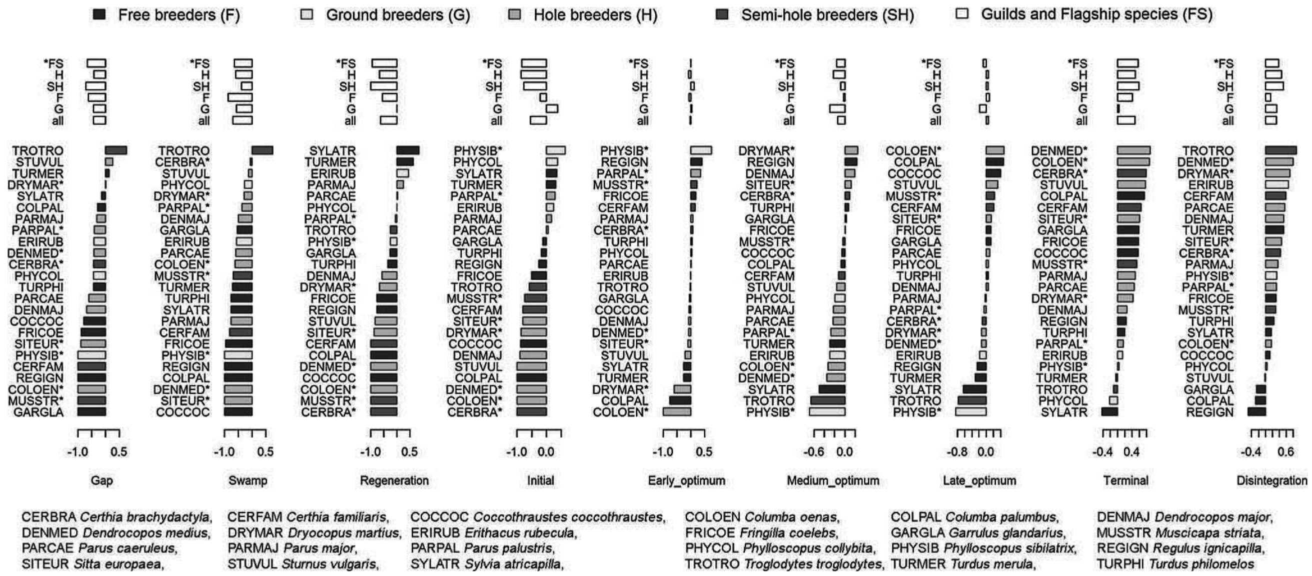


Fig. 4 Exemplary forest development phase (fdp) profiles of selected breeding bird species in lowland beech forests. *Y-axis* Mean Jacobs index per fdp for study sites, *asterisk* significant differences from zero (i.e. significant preference or avoidance of the respective fdp). Sample size per species is: *Erithacus rubecula* ($n = 18$ study sites), *Parus caerulus* ($n = 15$), *Sitta europaea* ($n = 13$), *Certhia familiaris* ($n = 9$), *Troglodytes troglodytes* ($n = 12$), *Phylloscopus sibilatrix* ($n = 7$), *Sylvia atricapilla* ($n = 14$), *Coccothraustes coccothraustes* ($n = 7$) and *Fringilla coelebs* ($n = 18$). *Sw* swamps, *Reg* regeneration phase, *Ini* initial phase, *EOp* early optimum phase, *MOp* medium optimum phase, *LOp* late optimum phase, *Ter* terminal phase, *Dis* disintegration phase

profile of habitat use in beech forests. Based on our data, bird species preferred and avoided different sets of several fdp (Fig. 4). Common Blackbird (*Turdus merula*) significantly preferred the regeneration phase, as did the European Robin (*Erithacus rubecula*) and Eurasian Blackcap (*Sylvia atricapilla*), but avoided the optimum phases as well as swamps. With respect to the Great Tit (*Parus major*), we did not find any significant preferences, but it did avoid the medium optimum phase, gaps and swampy parts. The Great Spotted Woodpecker (*Dendrocopos major*) significantly avoided all younger stages, namely, gaps, regeneration and the initial phase, as well as swamps. It also had no significant preference for any one fdp.

Importance of stand structure on the breeding bird community

Procrustes superimposition revealed that breeding bird community and three different stand structure parameters were highly reliable. The Procrustes coefficient was $t = 0.618$ ($p = 0.0019$) for similarity to fdp proportion, $t = 0.606$ ($p = 0.001$; Fig. 5) for similarity to mean fdp patch size and $t = 0.551$ ($p = 0.0036$) for similarity to patch number per fdp. Mean patch size was found to be important for the breeding bird community and for almost all single study sites; Procrustes residuals were comparably low (Fig. 5), except for a former shelterwood logging site (w4) and a managed stand with homogenous stand structure (w2). Furthermore, breeding bird composition was strongly related to fdp proportions, and only two stands with large amounts of medium (w2, 84 %) or late (r1, 66 %) optimum phase showed larger Procrustes residuals.

Discussion

Bird community

Our results show that the terminal and disintegration phase were preferred by most of the bird species studied (Fig. 3; Table 2). This preference became even clearer for single registrations: the later the position of the respective fdp in the forests' life cycle, the more the number of bird species which showed a preference for this phase. For the terminal and disintegration phase, 21 species showed positive Jacobs indices. This result is in line those of Schumacher (2005) who also reported a preference for the terminal and disintegration phases by breeding birds in lowland beech forests using the same definitions for fdp. Higher preference values in fdp with large trees and a high amount of deadwood might also be explained by a higher abundance and diversity of microhabitats (Winter and Möller 2008) as well as by higher invertebrate food availability (Moorman and Guynn 2001; Möller 2005; Lachat et al. 2012), both providing the main food supply during the breeding season and accommodating biodiversity (Lassauce et al. 2011).

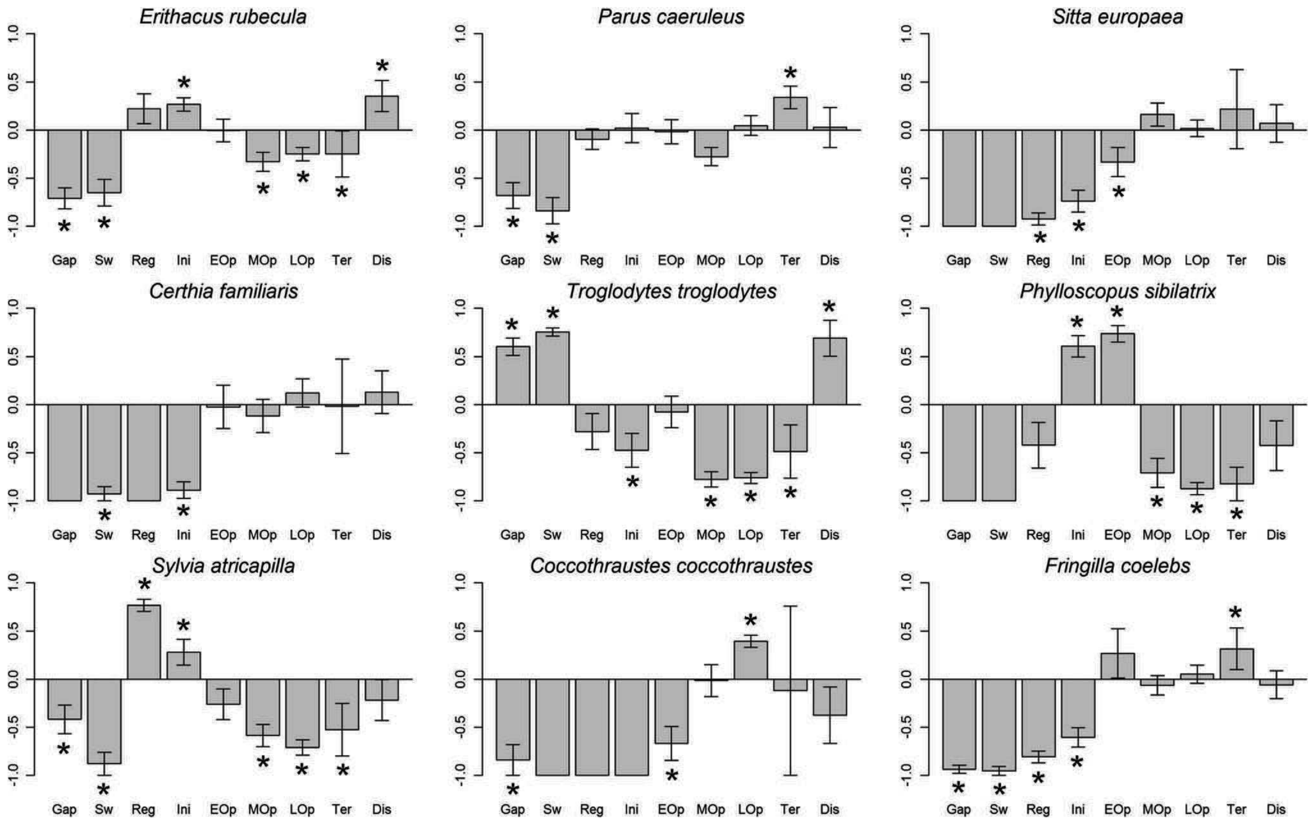


Fig. 5 Procrustes superimposition plot of 19 study sites for the first two dimensions. *Arrows* Residuals between bird abundance and mean fdp patch size of each site on the first two dimensions. Study site abbreviations: *r1−r3* Long-term unmanaged sites, *w3*, *k1−k4* recently unmanaged sites, *w4*, *w6* former shelterwood logging sites, *w1*, *w2*, *w7−w13* managed stands

The three optimum phases served as functional units as there were no significant differences in their respective median Jacobs indices across all 24 species. The regeneration phase seemed to play a more important role in territories for some species (Table 2). One possible explanation might be that some species, such as Chiffchaff (*Phylloscopus collybita*) and Song thrush (*Turdus philomelos*), often use song perches in proximity to but outside of the regeneration phase. When aggregated to minimum convex polygons these territories would then include a higher proportion of the regeneration phase.

Almost all ecological breeding guilds preferred the disintegration phase and terminal phase (Table 2; Fig. 3); ground breeders preferred only the latter, which might be explained by a more open character of the ground layer. Both analyses, habitat use by single registration data and by territory areas, showed similar tendencies (Table 2). Gaps and swamps were mostly avoided by all guilds (but preferred by single species, see below; Fig. 4). Early stages of growth were preferred only by ground breeders or free breeders, which use dense regeneration in the ground layer for nest construction, foraging and shelter (Moorman and Guynn 2001).The early and medium optimum phase might be avoided by ground breeders due to the lack of dense vegetation, and also by hole breeders (Głowaciński 1975; Smith et al. 1985; Ferry and Frochot 1990) as well as flagship species. One possible reason for this avoidance is the absence of structures for breeding, nest construction or foraging, such as scars, cavities, mold pockets or bark pockets with rich invertebrate diversity, in trees of this age (Winter and Möller 2008). Trees with large trunks potentially provide a high chance to develop various microhabitats and are, therefore, an important factor in determining habitat quality for hole-nesting species, such as Nuthatch and *Parus* species (Enoksson et al. 1995).

Compared to single registrations, preference for certain fdp was not as clear as for territories. We used these different ways of calculating habitat use to account for particular disadvantages. In single registrations, the bird is recorded only during activity and not when incubating a nest or sitting in a cavity. Furthermore, the recording might be more successful in some fdp (optimum phases, gaps) than in others (regeneration phase, disintegration phase) due to higher visibility. In contrast, the minimum convex polygon method includes territory parts that are not or only rarely used. Therefore, the combined interpretation of both allows a more balanced characterization of habitat use.

Single bird species

The species-specific profiles illustrate clearly that it was not only the presence of a late-stage fdp (like terminal and disintegration phase) that was important for most bird species, but rather a set of different fdp (Haila et al. 1989). Each species showed a particular combination of either preferred or avoided fdp (Fig. 4). Each fdp was also significantly preferred by at least one species, except for the medium optimum phase, which represented the largest proportion of managed beech forests in terms of area. In our study the medium optimum phase was not preferred by any bird species, a finding also reported by Schumacher (2005) for the breeding bird community of lowland beech forests.

According to Schumacher (2005) and Fuller (2000), the Eurasian Blackcap and Common Chiffchaff prefer gaps, while we quite often observed only the Common Chiffchaff singing in close vicinity to gaps. However, in contrast to our study design, Fuller (2000) included the regeneration phase into his definition of gaps, which may explain the preference of the Eurasian Blackcap for the regeneration phase in our data in contrast to the preference for gaps according to Fuller (2000). The Wood Warbler has been reported to be neutral towards gaps (Schumacher 2005) or to avoid them (Fuller 2000), as also suggested by our results. In contrast to other ground breeders, the Wood Warbler significantly preferred the early optimum and initial phases and was registered very often singing in these fdp. Marti (2007) found that the Wood Warbler prefers habitats with a complete canopy cover and tree sizes between 35 and 50 cm dbh, which is covered by the early optimum phase in our study. Ghadiri Khanaposhtani et al. (2012) reported that the Chaffinch (*Fringilla coelebs*) is associated with early successional stages and the Nuthatch prefers late successional stages. In our study, we found that the Chaffinch showed only a slight preference for the early optimum phase; however, our results do confirm the preference of the Nuthatch for late successional stages.

Stand structure

The results of our Procrustes analysis implies a link between the fdp proportion in a particular stand and the breeding bird communities inhabiting this stand. Procrustes correlation coefficients were similar for mean patch size and fdp composition, indicating that an appropriate presence (Haila et al. 1989) and texture of fdp within the forest stand is required (Haila et al. 1996; Heikkinen et al. 2004). Both are important for a certain heterogeneity within the forest structure (Mitchell et al. 2006; Hewson et al. 2011) and thus the breeding birds' habitat.

Large Procrustes residuals in some study sites (w2, w4; Fig. 5) might be explained by the surrounding landscape: the former shelterwood logging site w4 is enclosed by larger and older stands, which provide structural diversity and the presence of later fdp. The lower similarity of study site w2 refers to a monotonous composition of fdp accompanied by a high dominance of medium optimum phase, but we found relatively high species richness due to some species having only one territory within the study site. This relatively high species richness might be caused by surrounding gardens (Common Redstart *Phoenicurus phoenicurus*), some conifers in and close to the study site (Goldcrest *Regulus regulus* and Coal Tit *Periparus ater*), close proximity of farmland (foraging area for Red Kite *Milvus milvus*, Common Buzzard *Buteo buteo* and Tawny Owl *Strix aluco*) and close proximity of urban area (Common Starling *Sturnus vulgaris*).

Conclusions

We conclude that fdp integrate different key parameters that represent forest habitat conditions, such as food availability, light conditions, microhabitats, deadwood structures, shelter and microclimate, which in turn affect the distribution of breeding birds. In our study, we considered the most common 24 bird species, and the results clearly show that a combination of specific fdp is an important factor in the structural pattern of habitats for breeding birds. However, the terminal and disintegration phases do play an important role for most breeding birds. Additionally, our results suggest that fdp proportion (in terms of area) and patch size are strongly linked to the composition of forest breeding bird communities. Therefore, management schemes which ensure the simultaneous presence of different fdp at a small scale are making a major contribution towards the preservation of the biodiversity of breeding birds inhabiting beech forests. Our results provide a detailed look at species-specific differences on one hand and similarities within the bird community and ecological guilds on the other hand and may facilitate a better understanding of the relationship between breeding birds and fdp as an integrating tool to describe forest habitats.

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Conflict of interest None.

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ERRATUM

Erratum to: Forest development phases as an integrating tool to describe habitat preferences of breeding birds in lowland beech forests

Heike Begehold · Michael Rzanny · Martin Flade

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The figures and its captions were swapped by mistake during the production process and erroneously published in the official publication. The correct orders of figures are given below. We apologize for any inconvenience caused.

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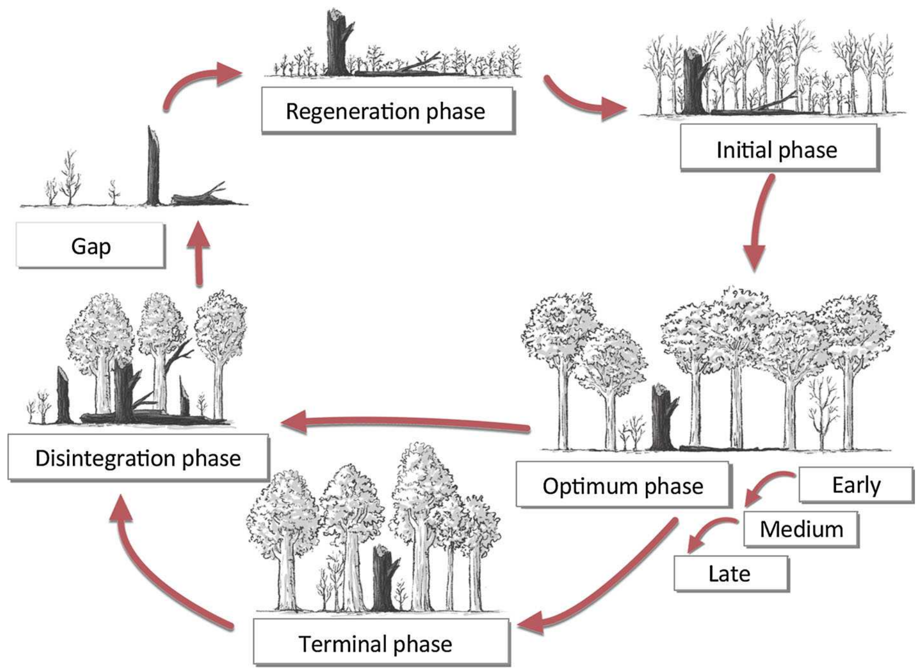

Fig. 1 Simplified model of the forest life cycle in beech forests. Early, medium and late optimum phases differ only in tree dimensions; for details see Table 1

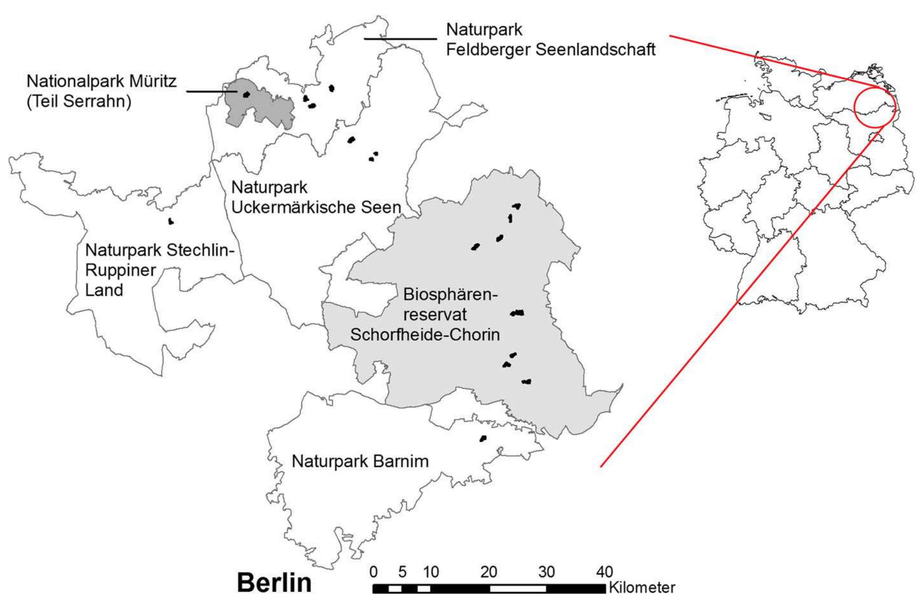

Fig. 2 Locations of the 19 study sites and large protected areas (national park, biosphere reserve, nature parks) in north-eastern Germany. *White* Nature parks, *shading in light gray* Schorfheide-Chorin Biosphere Reserve, *shading in dark gray* Müritz National Park

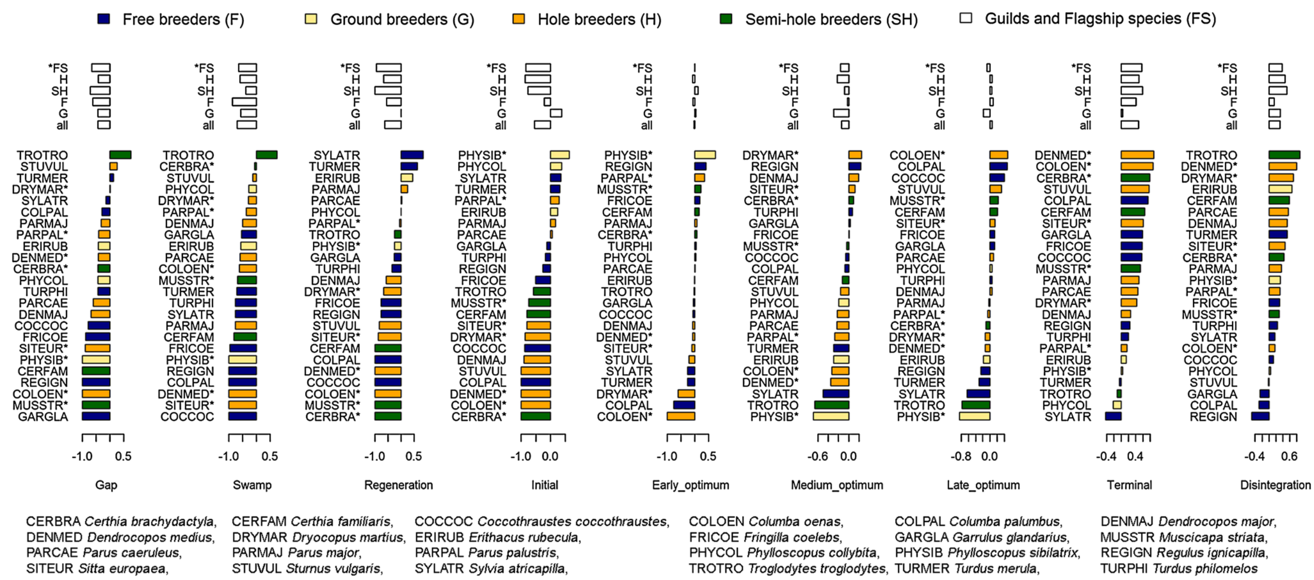

Fig. 3 Jacobs indices according to single registrations of breeding birds, ecological guilds (*yellow*) and among beech forest indicator species (*asterisk*; Flade 1994; Schumacher 2005). Included are 24 species each with more than 70 single registrations across all study sites. Species abbreviations are given as the EURING (European Union for Bird Ringing) code (*bottom of graph*)

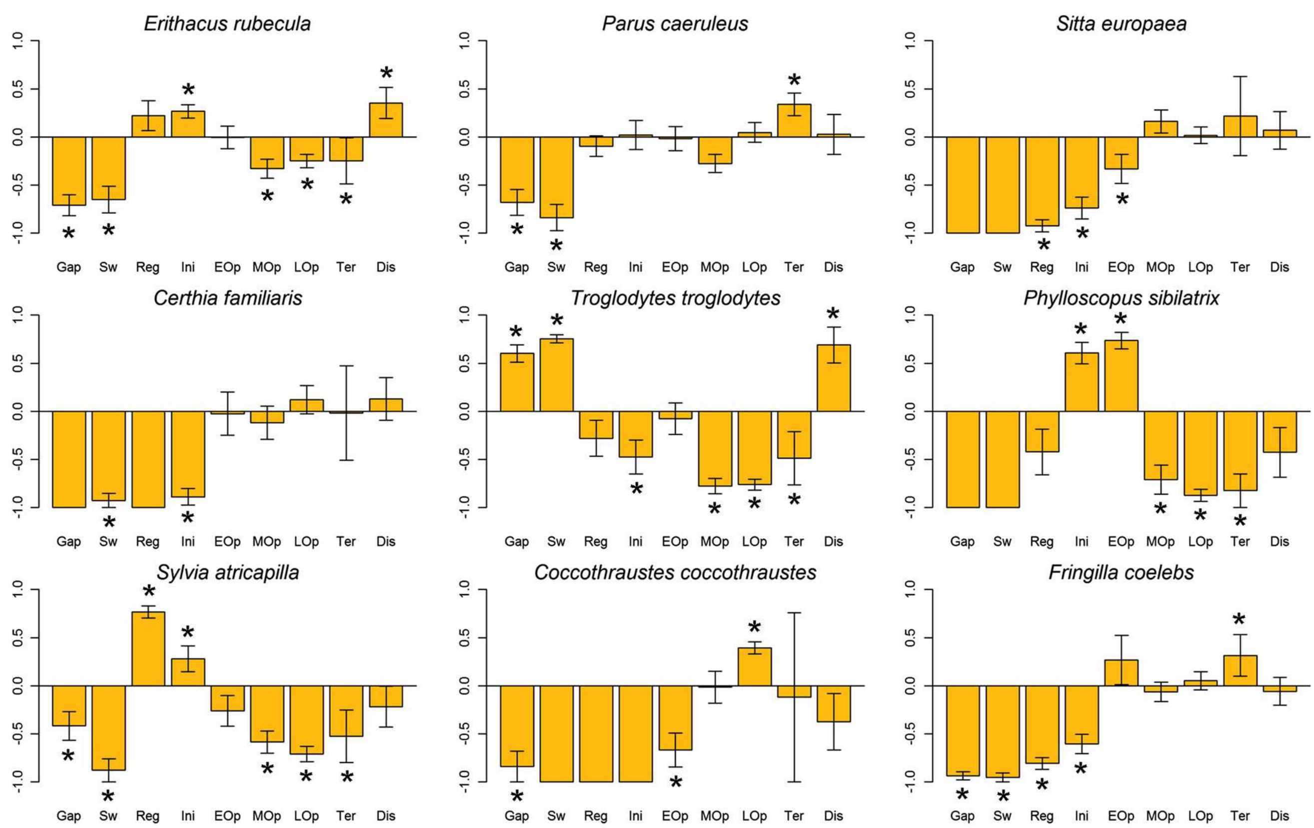

Fig. 4 Exemplary forest development phase (fdp) profiles of selected breeding bird species in lowland beech forests. *Y-axis* Mean Jacobs index per fdp for study sites, *asterisk* significant differences from zero (i.e. significant preference or avoidance of the respective fdp). Sample size per species is: *Erithacus rubecula* ($n = 18$ study sites), *Parus caerulus* ($n = 15$), *Sitta europaea* ($n = 13$), *Certhia familiaris* ($n = 9$), *Troglodytes troglodytes* ($n = 12$), *Phylloscopus sibilatrix* ($n = 7$), *Sylvia atricapilla* ($n = 14$), *Coccothraustes coccothraustes* ($n = 7$) and *Fringilla coelebs* ($n = 18$). *Sw* swamps, *Reg* regeneration phase, *Ini* initial phase, *EOp* early optimum phase, *MOp* medium optimum phase, *LOp* late optimum phase, *Ter* terminal phase, *Dis* disintegration phase

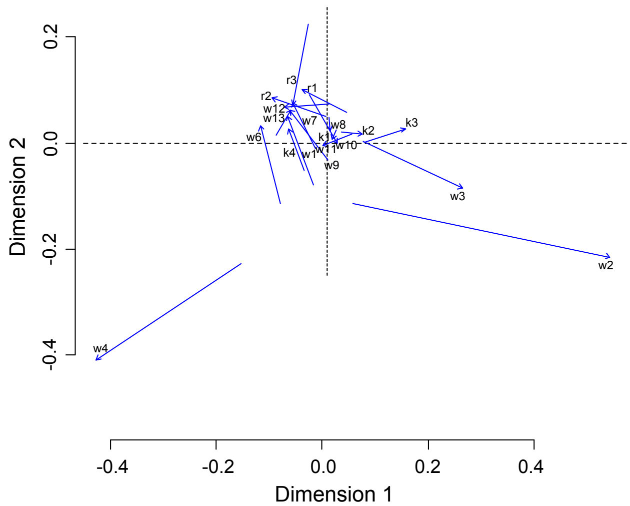

Fig. 5 Procrustes superimposition plot of 19 study sites for the first two dimensions. *Arrows* Residuals between bird abundance and mean fdp patch size of each site on the first two dimensions. Study site abbreviations: *r1*−*r3* Long-term unmanaged sites, *w3*, *k1*−*k4* recently unmanaged sites, *w4*, *w6* former shelterwood logging sites, *w1*, *w2*, *w7*−*w13* managed stands

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Patch patterns of lowland beech forests in a gradient of management intensity

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ABSTRACT

Forest development phases (FDPs) represent patches that are in different stages of the forest life cycle as conceived in the shifting mosaic concept. FDPs are a widely used framework to describe forest stand structure and dynamics. Natural forests are characterized by small patch sizes, a full set of FDPs and a large vertical heterogeneity which is considered crucial for their biodiversity. Forest management approaches that promote such characteristics of high naturalness are increasingly recommended for biodiversity conservation. Here we investigate the effect of a 10-year naturalness-promoting management regime on forest stand structure, expressed through different patterns in FDP structure and composition.

We studied 22 beech forest stands in north-eastern Germany that are managed in two different ways (naturalness-promoting management and other management) or that have been unmanaged for varying periods of time (recently, 20–35 years and long-term, 65 to more than 100 years). FDPs were investigated in 2012/13 across the total area of the study sites (714 ha). The FDP assignment is based on a dichotomic decision tree with variables such as diameter at breast height, canopy cover, deadwood amount, regeneration cover and tree height. We analyzed FDP patch size, aggregation and mean minimum distance between patches of the same FDP and structural evenness of FDP proportions.

For stands with naturalness-promoting management we found that: (1) there are different FDP proportions, FDP patch sizes and distances between patches of the same FDP compared to the other three management types; (2) there are significant differences in comparison to long-term unmanaged stands in terms of the aggregation indices of the initial phase, optimum phases and the disintegration phase; (3) these stands have the highest aggregation of the regeneration phase, which differs significantly from the other management types; and (4) they contain a similar FDP distribution to that in natural beech forests.

In conclusion, naturalness-promoting management supports small-scale patch heterogeneity and maintains forest structure and life cycle that are closer to natural and unmanaged stands compared to other management types.

1. Introduction

The structure of natural beech forests dominated by *Fagus sylvatica* L. is characterized by a fine-scaled mosaic of patches representing different phases of forest development (first mentioned by Watt, 1947). Concepts of the cycling process include temporal and spatial life cycle dynamics (Bobiec et al., 2000; Emborg et al., 2000; Korpel, 1995; Král et al., 2010; Mueller-Dombois and Ellenberg, 1974; Oldemann, 1990; Remmert, 1991; Winter, 2005; Winter and Brambach, 2011). The total stand area is divided into a number of forest development phase (FDP) patches, each running through cyclic succession processes, while these cycles are desynchronized among different patches (Wissel, 1992). Differences in the durability of the phases causes asynchrony and high unpredictability within the natural forest life cycle (Bobiec et al., 2000).

FDPs divide the forest life cycle into phases, which are each characterized by a specific combination of several structural parameters such as canopy cover, diameter at breast height (DBH), tree height, deadwood amount and regeneration cover. Thus, forest structure and condition can be spatially aggregated as a FDP mosaic across even large forest stands.

Two substantial components of the FDP mosaic patch concept, the spatial distribution and temporal sequence are also confirmed

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by forest dynamic simulations (Huber, 2011; Rademacher et al., 2004). The concept is applied for different purposes such as describing forest structure and dynamics (Diaci et al., 2011; Král et al., 2010; Kucbel et al., 2012; Schütz and Saniga, 2011; Winter and Brambach, 2011), serving as instrument for nature conservation (Bobiec et al., 2000) and for conducting biodiversity assessments (Boncina, 2000; Winter and Brambach, 2011). However the mosaic patch concept has also been seen critically (Gratzer et al., 2004; Paluch, 2007; Podlaski, 2008) because of a vulnerability to intermediate- or fine-scale disturbance events.

Global and European conventions such as the Convention on Biological Diversity (CBD, 1992), the Habitats Directive (92/43/EEC) and the biodiversity strategy of the Commission of the European Communities (2003) stipulate the protection and sustainable use of forests and conservation of their biological diversity. Several studies describe the impacts of management on biodiversity (e.g. overview Paillet et al., 2010; Rosenvald and Lõhmus, 2008; Winter et al., 2005); and forest biodiversity is strongly linked to the forest life cycle and the occurrence of certain FDPs (Michel and Winter, 2009; Müller et al., 2005; Winter and Brambach, 2011; Winter and Möller, 2008; Winter et al., 2005). Naturalness is an important criterion for nature conservation and for the preservation of global biodiversity (Reif and Walentowski, 2008; Winter, 2012), and integrating biodiversity conservation into forest use is a goal that is repeatedly demanded of contemporary forestry (Kraus and Krumm, 2013). Integrative forest management requires a near-natural stand structure in managed forests in order to maintain forest biodiversity (e.g. Christensen and Emborg, 1996; Flade et al., 2004; Kraus and Krumm, 2013; Lindenmayer et al., 2006; Rosenvald and Lõhmus, 2008; Suchan and Baritz, 2001; Winter et al., 2005). As such, forestry should aim to achieve a natural FDP patch distribution in order to provide the habitats required to promote biodiversity (Begehold et al., 2015; Boncina, 2000; Flade et al., 2004; Regnery et al., 2013; Suchan and Baritz, 2001; Winter, 2005; Winter et al., 2005). In sum, FDPs appear in forest ecology studies but, in terms of using FDPs as a monitoring variable, the knowledge of the spatial distribution as FDP proportions, patch sizes and aggregation as well as distances of FDP patches in unmanaged reference sites and in differently managed sites is exemplarily (studied in Suserup Skov, Denmark, by Christensen et al., 2007; Emborg et al., 2000; Emborg and Heilmann-Clausen, 2007 and in three beech study sites by Král et al., 2013). Spatial FDP distribution is a key aspect for migration of individuals, populations or communities (Townsend et al., 2000).

We analyzed differences between management types that (1) promotes naturalness, (2) other management forms as well as (3) recently and (4) long-term unmanaged stands with a focus on spatial distribution of the FDPs and structural FDP parameters such as FDP proportions, FDP patch aggregation and patch sizes. In order to compare the observed spatial distribution of FDPs with the hypothesized natural spatial distribution, we created a theoretical FDP distribution based on the lifetime of each FDP and compare structural patterns (FDP proportion) to those of single forest stands and management types.

We expect that management types differ from each other with regard to their FDP proportions, patch sizes and aggregation of FDP patches. Moreover, a gradient from managed to (long-term) unmanaged stands might become apparent. Further we expect that FDP proportions in long-term unmanaged stands are closest to the theoretical distribution, followed by naturalness-promoting management due to its adapted harvesting regime.

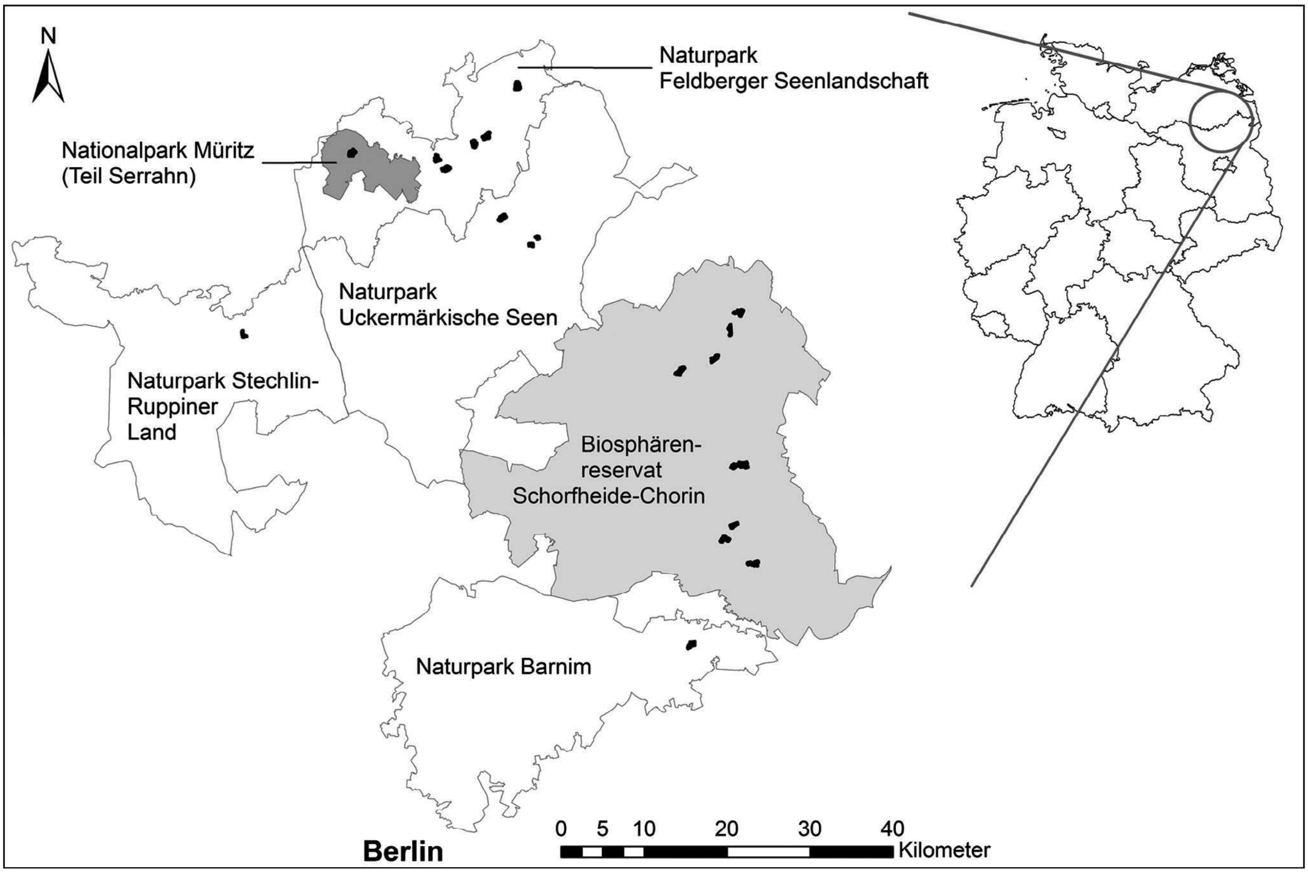

Fig. 1. Locations of the study sites and large protected areas (national park, biosphere reserve, nature parks) in North-eastern Germany (on the right hand, with federal states). White: Nature Parks, light gray: Schorfheide-Chorin Biosphere Reserve, dark gray: Müritz National Park.

2. Methods

2.1. Study area

Forest development phases were mapped in 2012 and 2013 in 22 lowland beech forests (Fig. 1). Three stands have been unmanaged for more than 63, about 100 and more than 100 years ('long-term unmanaged', r1–r3), eight stands have been 'recently unmanaged' since 1990 or 1998 (k1–k5, w3, w4, w6), and seven stands have been under a 'naturalness-promoting management' within the last decade (w7–w13, see also Table 1). Naturalness-promoting management considers preservation and interconnection of large trees and old-growth forest stands, layer complexity, deadwood amount and dimensions, conservation of microhabitats, natural regeneration and tree species composition (see also Table 2). These criteria have been put into concrete terms and are substantiated by specific threshold values (Flade et al., 2004; Winter et al., 2005). Finally, four stands were managed without a biodiversity focus. These are called 'differently managed' in the following text.

All study sites are mature stands and are at least 120 years old (two of the long-term unmanaged stands are more than 300 years old) and grow in mesotrophic soil conditions (Kopp and Schwanecke, 1994). They belong to three Fagetum associations. Most sites belong mainly to the mesotrophic Galio odorati-Fagetum, whereas the greater part of three sites belong to the Luzulo-Fagetum with more acidic soil conditions (Fischer, 1995). Some sites are partially covered by Hordelymo-Fagetum with more basic conditions. Study sites are located in the north-eastern part of Germany in the federal states of Brandenburg and Mecklenburg-Vorpommern between 52.8–53.3°N and 13.0–13.9°E. Climate conditions are similar at the study sites (continental according to Article 1c of the Commission of the European Communities, 2003): altitude varies between 43 and 130 m above sea level, mean annual precipitation is about 519–629 mm per year, mean annual temperature is 8.4–8.9 °C (DWD, 2013). Most stands are about 40 ha in size (30.4–44.9 ha), except for the two oldest sites (13.6 and 24.9 ha), two sites which have recently been unmanaged (12.3 and 20.1 ha) and two former shelterwood logging sites (unmanaged since 1998) (11.4 and 17.1 ha).

Table 2
Silviculture concept for naturalness-promoting management. For further explanations see Winter et al., 2003; Flade et al., 2004.

1. Silviculture methods that result in simple and largely homogeneous stand structures, such as shelterwood logging and clearcuts, are not applied. Management units are smaller than one hectare to allow for a heterogeneous stand structure. Gaps are welcome and not filled by planted regeneration. The forest is, or will be, multilayered and diversely structured
2. Five old trees per hectare (>40 cm DBH) are marked as habitat trees to let them develop microhabitats (Winter and Möller, 2008) with natural aging processes
3. A deadwood amount of at least 30 m^3 per hectare (in nature conservation areas of 50 m^3 per hectare) of standing and lying deadwood is provided in different dimensions (diameter >15 cm and length >3 m)
4. To preserve natural structures with habitat functions such as trees with broken crowns or broken trunks, trunks with lightning scars, trunk cavities, or bark pockets. At least 10 of 20 different microhabitat types as defined by Winter and Möller (2008) are present per hectare
5. The cutting threshold (trunk target dimension) should be at least 65 cm DBH
   Trees should be present with trunk diameters which are successively greater than 65 cm and moving towards those characteristic of very old habitat trees
6. Natural beech regeneration is used allowing for a near-natural mixture of indigenous tree species of around 15%
7. To determine, mark and maintain a permanent system of skid trails (with a distance of at least 40 m)
8. The water household is regenerated. Drainages are closed. Mires and wetlands are maintained within the forest

2.2. FDP mapping

During the winters of 2012 and 2013, we investigated FDPs in all study sites. We used a method developed by Tabaku (2000) modified by Winter (2005), who adapted it for easier usage in the field (see also Winter and Brambach, 2011). Therewith, FDP investigation illustrates the spatial characterization of a forest with the exact expansion and position of each FDP patch. Patches with an area of at least 196 m^2 were recorded according to a dichotomic decision tree that integrates different structural parameters (Table 3). We identified the patches in the field according to the given stand structure and shape within the forest stand. Our method is a dynamic frame method leaded by a marked 50 m × 50 m grid. The minimum FDP patch size of 196 m^2

Table 1
Study sites, sizes, management types. Differently = management without nature conservation focus, naturalness-promoting = management considering certain management criteria within the last decade (see Table 2). (For further information (altitude, precipitation, nutrition) see Winter, 2005, pp. 22, 150f).

Study site	Size (ha)	Name of the management type	Fagetum association (according to Fischer, 1995)
w1	34.0	Different	Galio odorati
w2	38.8	Different	Galio odorati
w21	38.8	Different	Galio odorati
w22	55.5	Different	Galio odorati
w3	42.0	Recently unmanaged (for 15 years)	Luzulo
w4	11.4	Recently unmanaged (for 15 years) and former shelterwood logging	Galio odorati
w6	17.1	Recently unmanaged (for 15 years) and former shelterwood logging	Galio odorati
w7	40.0	Naturalness-promoting	Galio odorati
w8	39.4	Naturalness-promoting	Galio odorati
w9	40.2	Naturalness-promoting	Galio odorati
w10	30.4	Naturalness-promoting	Galio odorati
w11	45.0	Naturalness-promoting	Galio odorati
w12	40.3	Naturalness-promoting	Galio odorati
w13	34.1	Naturalness-promoting	Luzulo
k1	20.1	Recently unmanaged (since 1980)	Luzulo
k2	36.5	Recently unmanaged (since 1990)	Galio odorati
k3	40.3	Recently unmanaged (since 1990)	Galio odorati
k4	13.6	Recently unmanaged (since 1990)	Galio odorati
k5	15.2	Recently unmanaged (since 1990)	Galio odorati
r1	43.1	Long-term unmanaged (since 1950)	Galio odorati
r2	24.9	Long-term unmanaged (at least since 1900)	Galio odorati
r3	13.6	Long-term unmanaged (at least since 1900)	Galio odorati

Table 3
Description of different FDPs according to stand parameters (following Winter, 2005; Winter and Brambach, 2011). An FDP patch is recorded with a minimum size of 14 m × 14 m. Canopy cover = canopy cover of all trees with DBH > 7 cm, DBH = diameter at breast height measured at the trunk height of 1.3 m, DBD_{max} = largest DBH within the investigated patch, deadwood = proportion of standing and lying deadwood from the total stock volume within the patch. Regeneration includes all tree individuals after the seedling stage and with DBH < 7 cm.

FDP	Parameters
Gap	Canopy cover < 30%, Regeneration cover < 50%, any deadwood amount
Regeneration phase	Canopy cover < 30%, Regeneration cover > 50%, any deadwood amount
Initial phase	Canopy cover > 30%, DBH < 20 cm, any deadwood amount
Early optimum phase	Canopy cover > 30%, 20 cm < $DBH_{max} \leqslant$ 40 cm, deadwood amount < 30%
Mid-optimum phase	Canopy cover > 30%, 40 cm < $DBH_{max} \leqslant$ 60 cm, deadwood amount < 30%
Late optimum phase	Canopy cover > 30%, DBH_{max} > 60 cm, deadwood amount < 30%
Terminal phase	Canopy cover > 30%, DBH_{max} > 60 cm, height > 85% of potential height (= 45 m), deadwood amount < 30%
Disintegration phase	Canopy cover > 30%, DBH > 20 cm, deadwood amount > 30%

(14 m × 14 m) is taken as a polygon frame for getting a core patch of a specific FDP using the dichotomic decision tree by measuring (DBH, tree height) or estimating (deadwood amount, canopy cover, regeneration cover) the relevant parameters. For the identification of the patches, the area of regeneration cover and canopy cover were assessed as more or less than 50% (for regeneration cover) or 30% (for canopy cover) of the patch area with the help of GPS. Standing and lying deadwood was measured (length, diameter) and crown deadwood was estimated. Deadwood amount was then determined as more or less than 30% of the total wood volume within the patch. Then, the core patch was enlarged until another 196 m^2 patch of another FDP neighbors the first polygon. This happens when one of the parameters of the defined FDP changed according to the first decision measurements (e.g. another DBH_{max}, deadwood amount, canopy cover, tree height, regeneration cover) indicating another FDP and therewith another FDP patch. The 50 m × 50 m grid is for orientation and grid borders can be overlapped by patches. We used GPS with an accuracy of ±1 m (corrected by differential GPS correction data). Accuracy changes within the relief of the sites (3–5 m), but patch position and extension was checked double from different positions of the patches. Hence, the entire study area was divided in a discrete number of FDP patches and transferred to a map showing the position, type and shape of each patch (Appendix 1).

2.3. Model of natural FDP distribution

For the FDP distribution model, we estimated the persistence of each FDP. The purpose of the model is to represent a reference, against which the observed FDP proportions can be compared, in order to link age periods of beech forest patches to a theoretical natural distribution of FDP proportions in an assumed forest. In a natural forest, all FDPs are present and according to their particular life time, including disturbances. According to the maximum life time of beech, these proportions were calculated to spatial proportions and taken as the model values. Therewith, FDPs cover the forest area with certain average spatial proportion. We mainly extracted information from local growth tables and studies in north-eastern Germany (to ensure regional comparability of the growth conditions such as climate and soil) as well as from other studies in European beech forests.

The maximum age of *F. sylvatica* is approximately 360 years in the lowlands based on the two beech reference sites in the lowlands (Knapp and Jeschke, 1991) and was set as 100% for the beech forest life cycle. The duration of gaps was taken as 7.5 years, the average of five to ten years reported by Knapp and Jeschke (1991) who studied the above mentioned two reference sites in north-eastern Germany. In other studies (Drößler and Meyer, 2006; Koop and Hilgen, 1987) a gap covers approx. 2% of the stand area which corresponds well with 7 years. Zeibig et al. (2005) reported 5.6% gaps corresponding to 20 years in natural beech forests. In the study of Zeibig et al. (2005) gaps were defined as a canopy opening, where regeneration might be present in the understory what is different to threshold of <30% that we used. For the following FDPs such as regeneration phase (17.5 years), initial phase (30 years, for consistency within other publications, we kept this terminology, although the term initial phase runs contrary to the idea of a cyclic concept), early optimum phase (45 years) and mid-optimum phase (50 years), we extracted growth dimensions from a growth model of beech in north-eastern Germany (Dittmar et al., 1986). For the regeneration phase, it corresponds to 4.7% (Drößler and Meyer, 2006) and for the biostatic optimal phase to 33–40% (Bobiec et al., 2000). The duration of subsequent FDPs (late optimum, terminal and disintegration phase) could not be calculated from the growth models as a result of age limits following harvesting recommendation. Therefore, we used the duration of the late optimum phase from a research project dealing with succession research in north-eastern Germany (von Oheimb et al., 2003). In this study, the relationship between

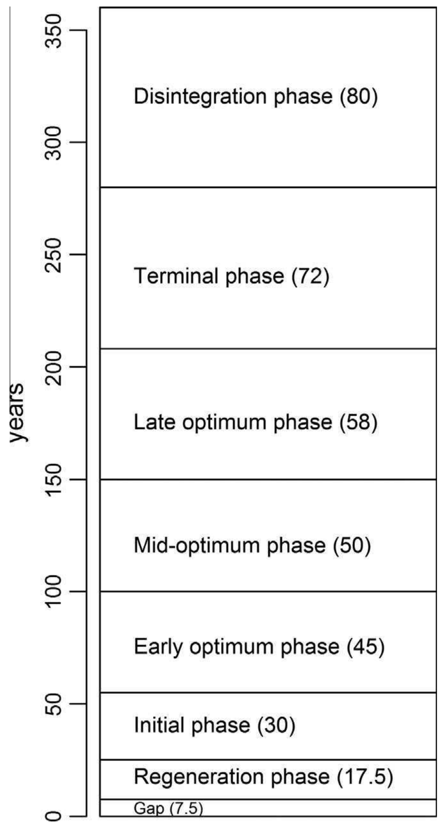

Fig. 2. Model of natural FDP distribution over the life time of a lowland beech forest stand. In parentheses the average number of years per FDP.

tree age and height was measured. There, the late optimum phase lasts up to an age of 208 years. Thus, in our model it starts at 150 years (duration of 58 years) then, at the point where the trees reach the height threshold between the two FDPs, the subsequent terminal phase starts (also here, for consistency, we kept this terminology, although and again the term "terminal" is not fitting into a cyclic concept). Estimates of the durations of terminal and disintegration phases were the most uncertain because only two stands in north eastern Germany (13.5 and 24 ha) have been unmanaged for more than 100 years allowing the development of a natural stand structure. Knapp and Jeschke (1991) state that the disintegration phase could possibly last for 100 years. This includes the gap and at least partially the regeneration phases as per our definition. Thus, a period of 80 years might be appropriate for the disintegration phase, which also corresponds to Král et al. (2014) who report a covering proportion of 10–25% of the stand area for the breakdown stage. This prolongs the terminal phase to 72 years, which corresponds to Bobiec et al. (2000) and with the 200 year-duration of the mid-optimum, late optimum and terminal phases (Knapp and Jeschke, 1991), as well as with the 150 year duration for the terminal and disintegration phases identified by Meyer et al. (2003).

2.4. FDP structure within a stand: FDP proportions and patchiness

Patch size was calculated for each FDP patch on all study sites. The proportion and mean patch size of each FDP were summarized using Principal Correspondence Analysis (PCA) and standardized data to weight all parameters equally. Further, for each study site we identified all distances between patches of the same FDP, calculated as minimal distances between patch edges. The smallest distances connecting all FDP patches per study site were computed using the minimum spanning tree algorithm. Using the mean minimum distances between patches of the same FDP per study site, we calculated a non-metric multidimensional scaling (NMDS) ordination based on Gower dissimilarity. NMDS was performed with three axes and resulted in stress values of <0.1.

To compare the FDP structure among the study sites and with the structure predicted by the model, we calculated the structural evenness in terms of FDP proportions. We used Pielou's evenness index (Pielou, 1966) which quantifies how equal the different FDP proportions are within a stand. Based on this index we compared the relative differences among the study sites and the model:

(1) $J' = \frac{H'}{H'_{max}}$, where H' is the number derived from the Shannon diversity index (Shannon, 1948) and H'_{max} is the maximum value of H', equal to:

(2) $H'_{max} = -\sum_{i=1}^{S} \frac{1}{S} \ln \frac{1}{S} = \ln S$, where S is the total number of FDP present. J' varies between 0 and 1, where a value of 1 symbolizes an exact uniform distribution of FDPs or equal FDP proportions.

We used the Index of Aggregation R (Clark and Evans, 1954) to determine the spatial distribution of FDP patches. R was calculated for each study site and summarized for each management type. A value of $R = 0$ indicates that the patches are maximally aggregated. As R increases, the degree of aggregation decreases. If R is about

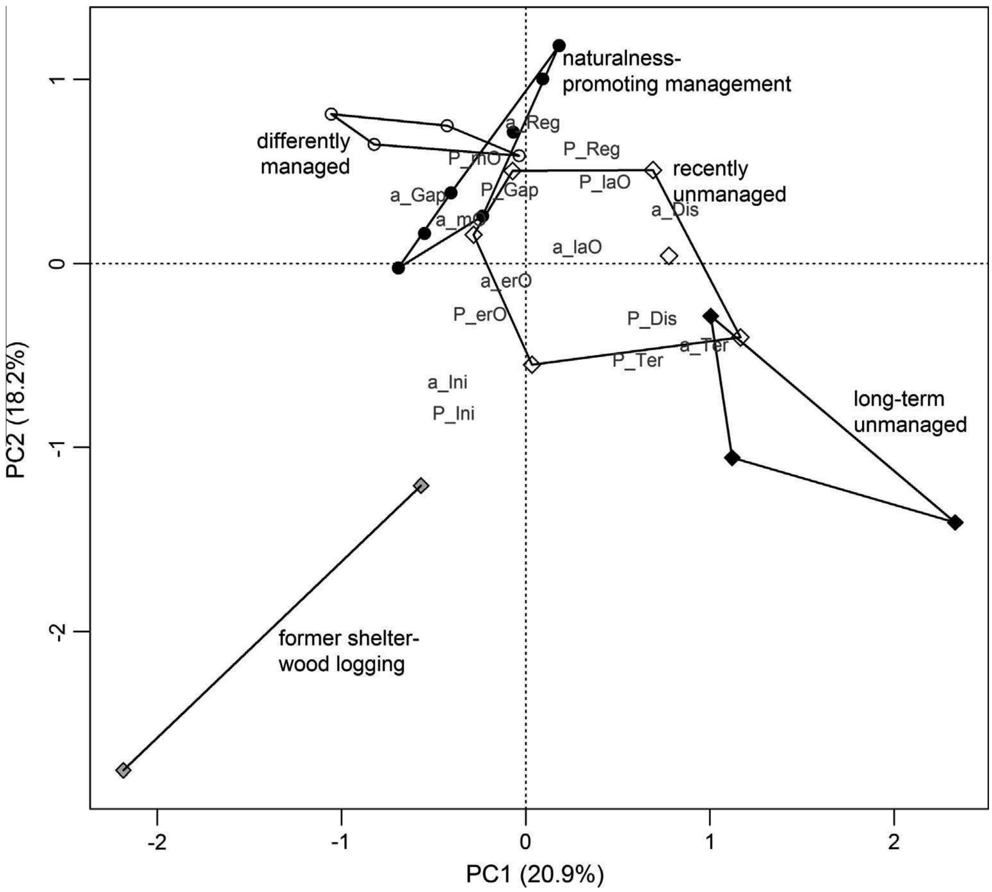

Fig. 3. Graphical display of the Principal Correspondence Analysis concerning FDP structure of 22 study sites. Included are the parameters of mean patch sizes per FDP (a) and FDP proportions (P). Reg = Regeneration phase, Ini = Initial phase, erO = Early optimum phase, mO = Mid-optimum phase, laO = Late optimum phase, Ter = Terminal phase, Dis = Disintegration phase.

one, it indicates a random patch distribution. Larger values of R indicate a uniform or regular patch distribution. R was calculated for each study site and FDP. The following equation was used to determine R for a FDP sample per study site:

(3) $R_i = mmd_i \cdot 2\sqrt{n_i/A}$ with mean minimal distance according to the minimum spanning tree algorithm of the i-th FDP (mmd), number of patches of the i-th FDP (n) and the total area of the study site (A).

The 95% confidence intervals were calculated for each management type and were compared among them and with the model value.

All data was prepared in ArcGIS 9.3.1. All calculations and graphics were computed in R (R Core Team, 2012) using the package vegan (Oksanen et al., 2013) and compositions (Van den Boogaart et al., 2013).

3. Results

3.1. FDP reference model

According to the model built in the methods (Section 2.3), we here present the model of FDP durations (Fig. 2).

3.2. FDP structure in forests with different management intensity

The FDP structure represented by FDP proportions and FDP patch sizes varies according to the management intensity, thus the study sites are ordered accordingly (Fig. 3, Appendices 2 and 3). When using these data to calculate a PCA, its first axis strongly reflects the management gradient (Fig. 3). Managed study sites vary between a dominance of mid-optimum phases (patch size and proportions, differently managed study sites) and a wider variability of younger phases such as gaps, regeneration and initial phases (naturalness-promoting management). Former shelterwood logging sites are dominated by large patches of the initial phase, which have grown within the last 15 years. For this reason they are isolated from the other study sites in the PCA diagram (Fig. 3). Recently unmanaged study sites are grouped around parameters of the three optimum phases, gaps and the older phases such as the terminal and disintegration phases. As the time since management abandonment increases, FDPs with larger trees and more decay (terminal and disintegration phases) become more important. As such, long-term unmanaged study sites are characterized by higher proportions and patch sizes in FDPs such as the terminal and disintegration phases.

The number of patches per hectare varied between management types (Appendix 3): highest patch numbers occur in long-term unmanaged stands with an average of 13.7 (range of 13.3–14.2) patches per hectare with a mean patch size of 730 m^2. This is followed by stands under naturalness-promoting management with a mean of 7.9 (6.3–10.4) patches per hectare with a mean patch size of 1265 m^2, and then recently unmanaged sites with an average of 6.9 (4.6–9.9) patches per hectare with a mean patch size of 1450 m^2. One study site, which has been unmanaged for more than 63 years, has an average of 6.3 patches per hectare (patch size 1587 m^2). Differently managed sites show the lowest

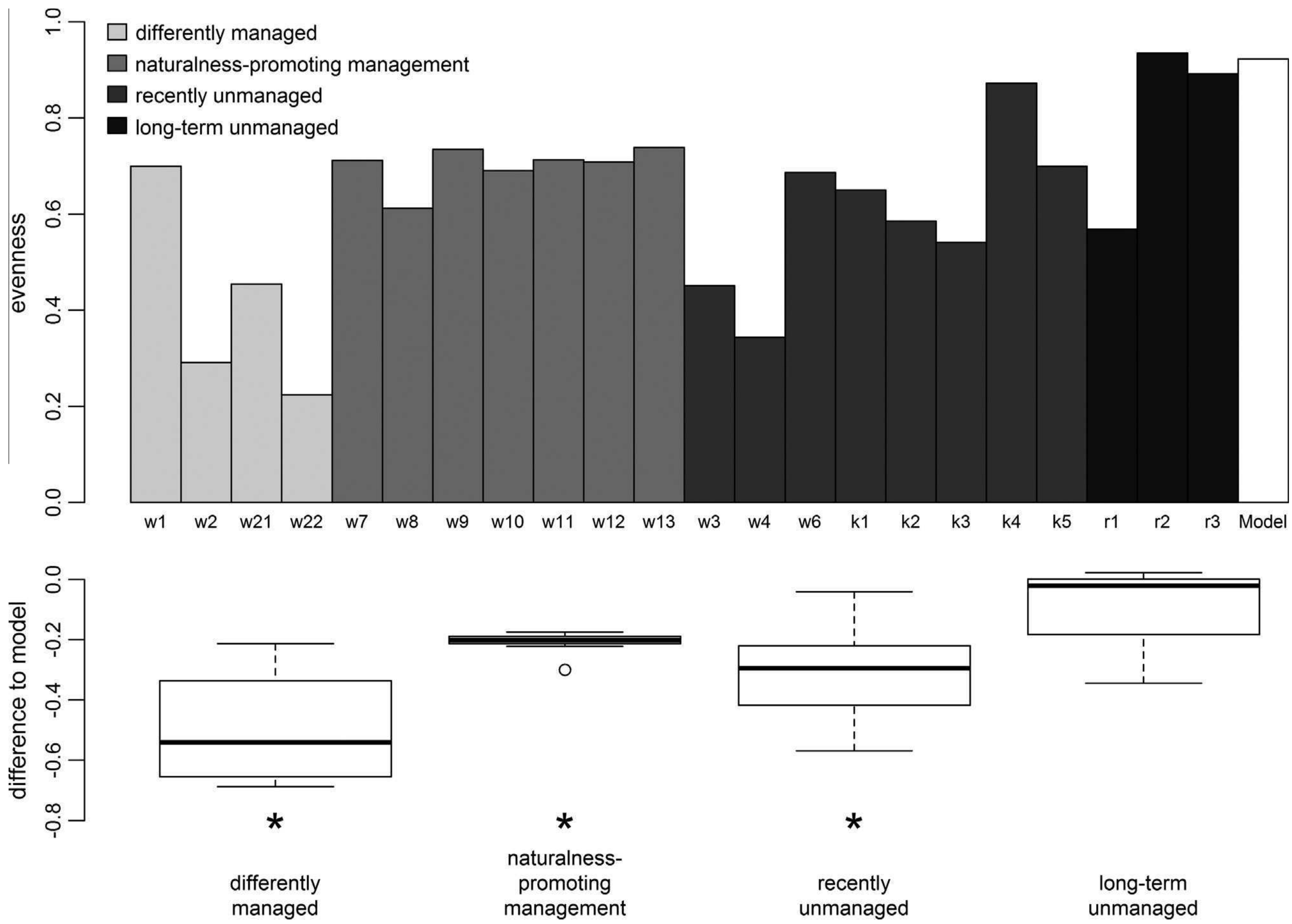

Fig. 4. Evenness of FDP proportions of 22 beech forest stands (named w1–r3) based on FDP proportions in comparison to the compiled model (above) and median relative evenness of management types in reference to the model (below). Asterisks symbolize significant differences between the management type and the model value.

patchiness value with 3.8 (2.1–7.3) patches per hectare (mean patch size of 2630 m^2). The variance within recently unmanaged study sites is relatively large due to a high dominance of just one FDP, which acts as a stand matrix of large size. Amongst differently managed stands, just one study site has a higher patchiness (Appendix 3).

The structural evenness of the FDP proportions varied only slightly in stands under naturalness-promoting management (median of around 0.712) and differs significantly from the value of 0.372 found in differently managed sites ($p = 0.02$, Fig. 4). Recently unmanaged stands show lower values for evenness (median of 0.618). For these three management types, the median structural evenness values differs significantly from the values of the two long-term unmanaged stands ($p < 0.009$) and from the model value. Long-term unmanaged stands have a similar evenness value to that of the model.

3.3. FDP patch distances and aggregation within the forest stand

We did not find a clear gradient across management intensity in terms of the mean minimum distances between patches of the same FDP. However, the NMDS shows a slight differentiation across management types (Fig. 5); study sites of the same management type are grouped together and can be differentiated from other groups with only a small overlap. Thus, distances between patches of the same FDP are rather similar within a management type (see also Appendix 4).

Aggregation indices vary among FDPs and management types (Fig. 6, Appendix 5): Gaps are almost randomly distributed across all management types (Fig. 6a). In the regeneration phase, patches are aggregated under naturalness-promoting management, which differs significantly from the other management types, where this phase shows a random or a slight shift towards an equal distribution (Fig. 6b). For initial phase patches, long-term unmanaged stands show an aggregation, which is significantly different from the other management types, where it is randomly or more equally distributed (Fig. 6c). Patches of the three optimum phases are differently distributed only for long-term unmanaged study sites (Fig. 6d–f). Here, aggregation differs significantly from naturalness-promoting (mid- and late optimum phases) or different management (early optimum phase) and additionally from recently unmanaged sites (early and mid-optimum phases). Moreover, patches are randomly distributed (early optimum phase) with a tendency towards aggregation (naturalness-promoting management) or are more strongly aggregated than in long-term unmanaged study sites (mid- and late optimum phases). Mid-optimum phase patches show the strongest aggregation of all FDPs, as they contain the largest patch sizes and proportions in managed and recently unmanaged study sites. The late optimum phase is aggregated most strongly under naturalness-promoting management (Fig. 6f). The distribution of terminal phase patches, which occurred frequently enough for analysis only in unmanaged stands, is higher in long-term than in recently unmanaged study sites (Fig. 6g). For the disintegration phase, patch distribution follows the management gradient: Patches are aggregated in long-term unmanaged study sites, which differ significantly from the other management types. This phase shows a random distribution in recently unmanaged study sites and more equal distribution in managed sites (Fig. 6h).

4. Discussion

4.1. FDP patterns follow a clear management gradient

The differentiating effect of different management types and varying times since management abandonment on FPD structure

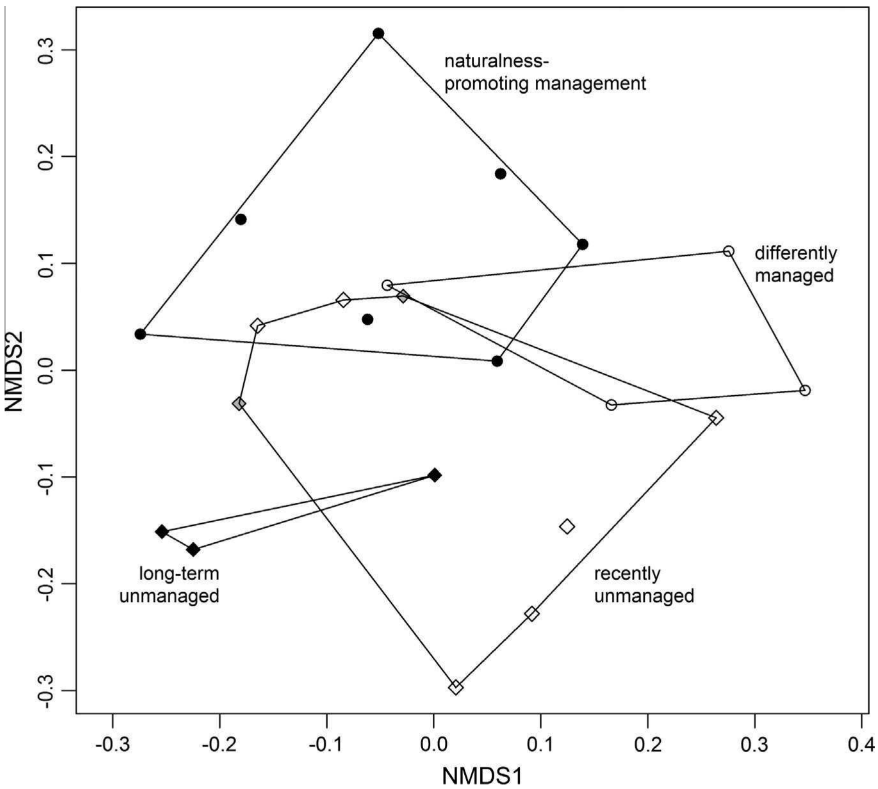

Fig. 5. Graphical display of the NMDS ordination of the study sites (points) and management type (polygons) based on the mean minimum distances between patches of the same FDP in lowland beech forests. The gray squares symbolize the two recently unmanaged former shelterwood logging sites.

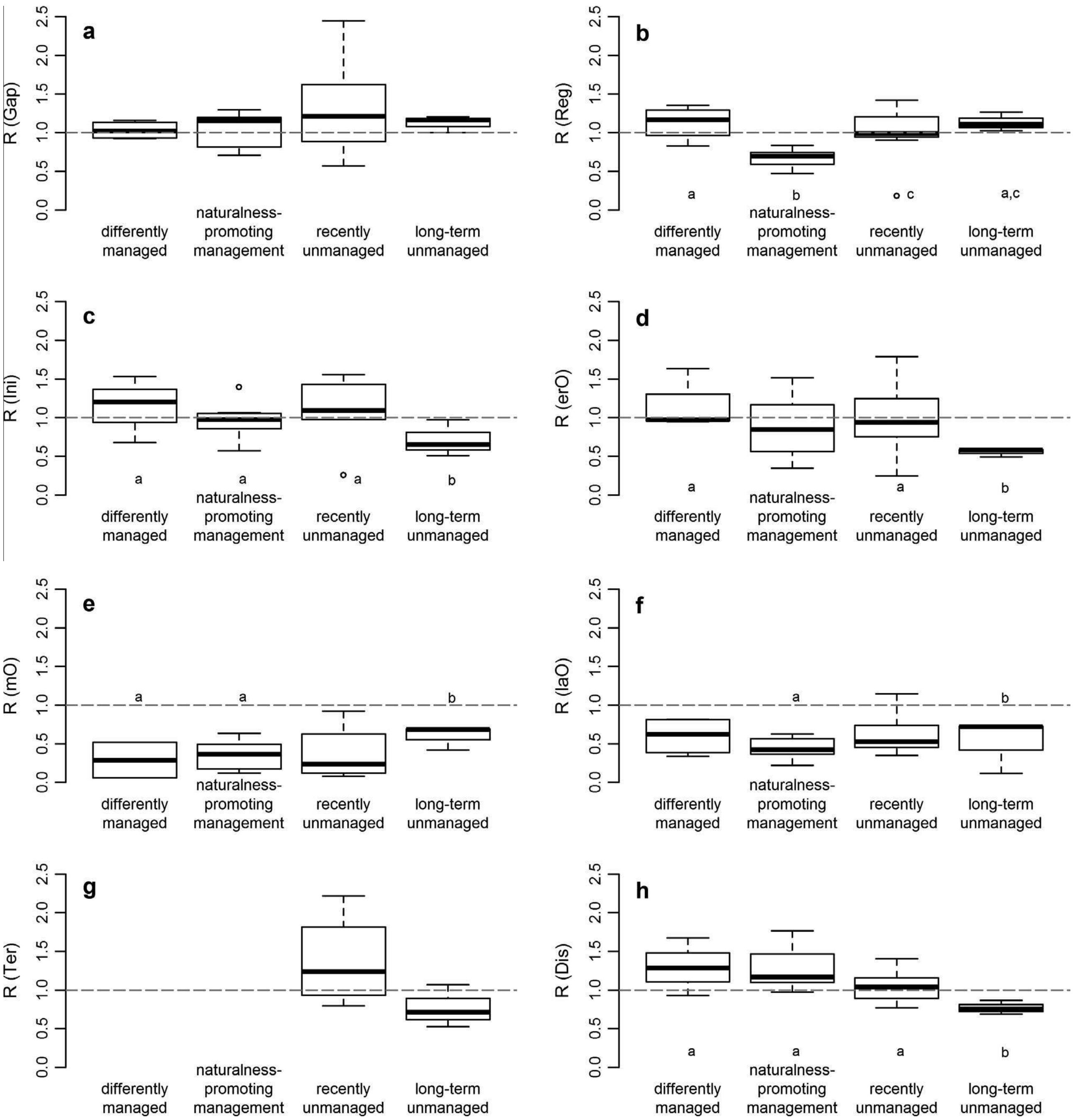

Fig. 6. Aggregation index R for different FDPs and management types of 22 lowland beech forest sites. Values of 0 symbolize maximum aggregation, values of about 1 (dashed line) symbolize random distribution of the FDP patches and values above 1 symbolize an increasingly even patch distribution. Reg = Regeneration phase, Ini = Initial phase, erO = Early optimum phase, mO = Mid-optimum phase, laO = Late optimum phase, Ter = Terminal phase, Dis = Disintegration phase.

characterized by FDP patch size and proportions is underlined by the grouping that was identified using the FDP proportion and patch size data, the structural evenness of FDP proportions and the minimum distances between FDP patches (Figs. 3–5). This has also been reported by other studies (Bobiec et al., 2000; Boncina, 2000; Christensen and Emborg, 1996; Heiri et al., 2009). The aggregation of single FDPs shows varying distribution patterns for the different management types (Fig. 6b–d) and emphasizes the unique position of the long-term unmanaged stands, especially those that have been unmanaged for more than 120 years.

In many studies, a clear difference between managed and unmanaged forest stands was found in relation to forest biodiversity (e.g. Christensen and Emborg, 1996; Corona et al., 2011; Paillet et al., 2010) and forest structure (Boncina, 2000; Emborg et al., 2000; Král et al., 2014). Our results show a clear differentiation of FDP structure as a consequence of different management types (Fig. 3) and assume different biodiversity accordingly. Moreover, we verify the importance of both the structural FDP parameters for the characterization of forest stands and their structural diversity: FDP proportions *and* mean patch sizes per FDP.

Some study sites differ slightly in the characteristics shown by the other sites of the same management type. An example of this is one long-term unmanaged site, which has been managed more recently than the other two sites in its grouping. The structural patterns of FDP proportion, patch sizes and patch mean minimum distances in this site are close to those in recently unmanaged sites

(Figs. 3 and 5). Thus, the expected transformation towards a small-scale mosaic of the different FDPs appears to take longer than the time which has elapsed since the cessation of management (Heiri et al., 2009; von Oheimb et al., 2005).

4.2. The particular importance of naturalness-promoting management

Our results show that after a decade of naturalness-promoting management the FDP structure is already distinguishable from the other management types: Patch sizes are smaller and provide a higher diversity of FDPs compared to the differently managed study sites (Figs. 3 and 4, Appendix 2). With only minimal development of the formerly homogeneous stand structure, as a result of an absence of management in recently unmanaged study sites, FDP composition did not change significantly over the last decade. As such, the structural evenness is lower than in stands under naturalness-promoting management. For the latter, aggregation of regeneration phase patches is highest (Fig. 6b) and shows a similar distribution to that found in natural European beech forests (Paluch, 2007). This underlines the assumed positive effect of the silviculture concept of naturalness-promoting management with eight different measures (Table 2) applied during the last decade. Thus, naturalness-promoting management mirrors the natural regeneration process and can lead to types of continuous cover forests (Dauerwald) (Commarmot et al., 2005). Moreover, it can also provide an economical alternative to other management regimes (Nord-Larsen et al., 2003). Although certain FDPs such as terminal or disintegration phases still occasionally occur in managed study sites (see also Christensen and Emborg, 1996), a higher proportion of the latter is found under naturalness-promoting management.

4.3. Patch patterns: Aggregation of different FDPs and patch sizes

FDP patch distribution patterns in managed beech forests are poorly studied. Mean distance between patches of the same FDP represent a crucial factor for the survival and reproduction of flightless and flight-limited species groups unable to move over long distances (e.g. some saproxylic beetles such as *Osmoderma eremita*, that cannot overcome distances greater than 300 m (Hedin, 2003)).

Our results show that for long-term unmanaged study sites, aggregation of patches of the same FDP was similar (see also Král et al., 2014) given that the variation amongst these sites is small for all FDPs except the late optimum phase (Fig. 6). Dominant phases such as the mid- and late optimum phases were always aggregated independent of the management type (Fig. 6e and f). This confirms the findings of other studies (Král et al., 2014), but contrasts with the random distribution of canopy trees found by Paluch (2007). Similar patterns can be partly caused by dependencies amongst them (Riitters et al., 1995): More abundant FDPs tend to have either larger patch sizes or higher connectivity (Král et al., 2014) which means they show smaller minimum distances which in turn reduces the value of the aggregation index (formula 3). FDPs such as the terminal and disintegration phases are most aggregated in long-term unmanaged study sites. This corresponds with the clumped distribution of giant trees (DBH > 80 cm) that is a characteristic of the terminal phase, and the aggregation of both standing and fallen dead wood in three Albanian virgin beech forests (Meyer et al., 2003) and standing entire dead trees and uprooted trees in a near natural beech forest in north-eastern Germany (von Oheimb et al., 2007) as features of the disintegration phase with >30% deadwood.

We found a mean patch size of 730 m^2 (200–1200 m^2) in long-term unmanaged stands which corresponds with other studies: Král et al. (2014) distinguishing four FDPs found mean patch sizes between 570 and 800 m^2. Emborg et al. (2000) report a mean patch size of 834 m^2 in 1992 which was confirmed by Christensen et al. (2007) ten years later (809 m^2) for five FDPs. Drößler and Meyer (2006) and Tabaku (2000) described for nine FDPs in Slovak, German and Albanian virgin beech forests mean patch sizes around 300–460 m^2. Christensen and Emborg (1996) found a typical patch size of 500–1500 m^2 in natural deciduous forest dominated by European beech. And even already Korpel (1989) described 200–700 m^2 as the area of the basic stand textural elements. Mean patch sizes vary across different FDPs (Emborg et al., 2000; Král et al., 2014). Patch sizes of FDPs with shorter temporally presence such as gaps or regeneration phases as well as terminal and disintegration phases are the smallest (Appendix 3), which is in line with Christensen et al. (2007), Drößler and Meyer (2006) and Král et al. (2014).

5. Conclusion

Our results show that forest structure can be distinguished by using FDP patterns such as proportion, patch sizes and patch distances as well as patch aggregation, which in turn depicts a gradient in management intensity. Naturalness-promoting management can at least partially create FDP patterns, which are typical of unmanaged stands. Further, our results confirm the specific role of patchiness and FDP proportions in long-term unmanaged, near-natural stands. FDPs integrate different key parameters that represent forest habitat conditions and represent a valid indicator for describing forest dynamics. Therefore, this concept might be useful for nature conservation monitoring assessments. In conclusion, forest management can be evaluated via FDP records, thus FDPs might be used, for example, for the assessment of the nature conservation status of Natura 2000 – centerpiece of the European biodiversity conservation policy – and for verifying the favorable conservation status as required by the habitat directive (92/43/EEC). Given that forest biodiversity is linked to the FDPs, FDP investigation would be a simple means of monitoring changes in forest biodiversity. Further studies are necessary in order to assess the context of FDP and species diversity.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.10.021.

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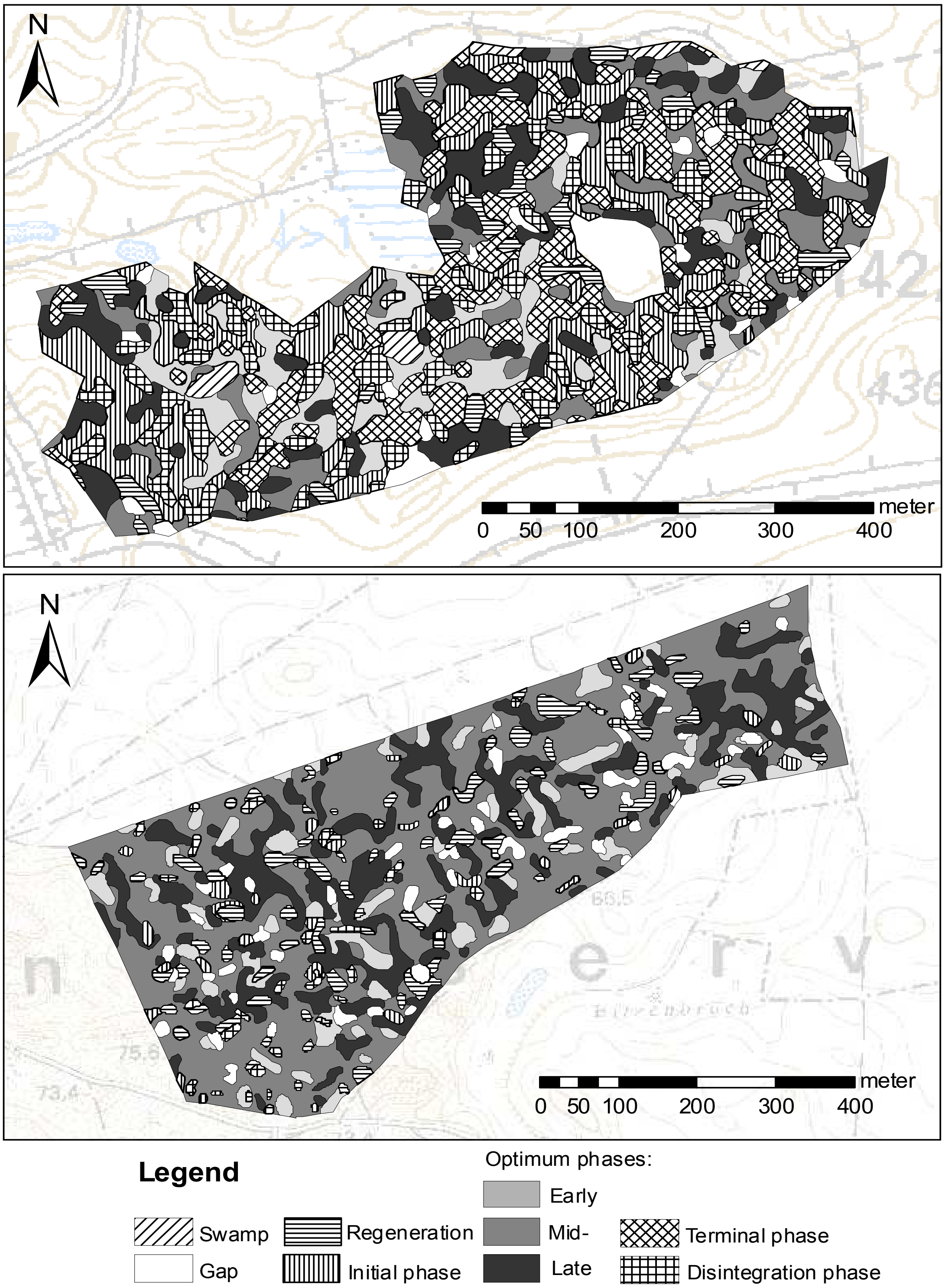
SUPPLEMENTARY MATERIAL



Appendix 1 FDP maps of study site r2 (above) and w10 (bottom). FDPs were determined directly in the field with a minimum patch size of 196 m^2. For further explanations see section 2.2

Appendix 2 Relative FDP proportions in 22 study sites and management types: [1]different management, [2]naturalness-promoting management, [3]recently unmanaged, [4]recently unmanaged and former shelterwood logging, [5]long-term unmanaged. Abbreviations of FDPs are explained in Fig. 3.

Study site	Gap	Reg	Ini	erO	mO	laO	Ter	Dis
w1[1]	0.04	0.07	0.18	0.03	0.20	0.47	0.00	0.01
w2[1]	0.03	0.02	0.01	0.00	0.85	0.09	0.00	0.00
w21[1]	0.04	0.02	0.01	0.02	0.67	0.24	0.00	0.01
w22[1]	0.01	0.01	0.00	0.00	0.88	0.10	0.00	0.01
w7[2]	0.03	0.19	0.13	0.01	0.17	0.45	0.00	0.02
w8[2]	0.03	0.08	0.01	0.04	0.47	0.35	0.00	0.02
w9[2]	0.02	0.19	0.15	0.03	0.30	0.30	0.00	0.01
w10[2]	0.05	0.08	0.03	0.09	0.50	0.24	0.00	0.02
w11[2]	0.02	0.08	0.05	0.18	0.45	0.20	0.00	0.01
w12[2]	0.07	0.03	0.04	0.39	0.25	0.22	0.00	0.00
w13[2]	0.03	0.06	0.08	0.36	0.31	0.15	0.00	0.01
k1[3]	0.03	0.06	0.03	0.07	0.52	0.26	0.00	0.02
k2[3]	0.01	0.01	0.01	0.04	0.51	0.34	0.03	0.04
k3[3]	0.01	0.02	0.00	0.02	0.58	0.29	0.03	0.04
k4[3]	0.09	0.07	0.21	0.05	0.30	0.17	0.01	0.11
k5[3]	0.01	0.02	0.01	0.26	0.40	0.23	0.02	0.05
w3[3]	0.01	0.02	0.03	0.01	0.71	0.19	0.00	0.03
w4[4]	0.01	0.00	0.79	0.04	0.14	0.02	0.00	0.00
w6[4]	0.01	0.00	0.44	0.13	0.20	0.19	0.00	0.03
r1[5]	0.02	0.03	0.09	0.01	0.11	0.67	0.02	0.05
r2[5]	0.03	0.05	0.19	0.10	0.14	0.15	0.22	0.13
r3[5]	0.03	0.04	0.07	0.22	0.29	0.16	0.09	0.11

Appendix 3 Mean patch sizes (MPS) over all patches and for each FDP (± standard diviation) in 22 study sites and management types: [1]different management, [2] naturalness-promoting management, [3] recently unmanaged, [4] recently unmanaged and former shelterwood logging, [5] long-term unmanaged. Abbreviations of FDPs are explained in Fig. 3.

Study site	MPS [ha]	MSP [sqm]							
		Gap	Reg	Ini	erO	mO	laO	Ter	Dis
w1[1]	0.14 (0.53)	340.9 (0.02)	743.7 (0.07)	1495.3 (0.32)	1058.0 (0.13)	1607.8 (0.28)	2302.7 (0.94)	--	272.9 (0.01)
w2[1]	0.35 (3.09)	379.7 (0.03)	390.0 (0.02)	534.0 (0.03)	357.5 (0.01)	109210.0 (18.86)	729.4 (0.10)	--	305.0 (0.00)
w21[1]	0.34 (2.18)	486.6 (0.03)	478.6 (0.02)	526.0 (0.02)	1092.9 (0.05)	36522.9 (8.55)	2050.7 (0.37)	--	392.0 (0.02)
w22[1]	0.56 (4.73)	411.4 (0.02)	421.4 (0.01)	320.0 (0.00)	350.0 (0.02)	229565.0 (32.43)	891.8 (0.10)	--	309.1 (0.01)
w7[2]	0.13 (0.49)	418.3 (0.04)	845.6 (0.09)	1181.6 (0.15)	482.5 (0.02)	1209.3 (0.14)	2988.1 (1.09)	---	312.3 (0.01)
w8[2]	0.15 (0.60)	349.7 (0.02)	550.2 (0.04)	697.5 (0.07)	456.8 (0.02)	6171.7 (1.67)	1799.5 (0.24)	--	319.5 (0.01)
w9[2]	0.11 (0.24)	300.5 (0.01)	843.5 (0.08)	1216.3 (0.12)	691.3 (0.07)	1601.5 (0.48)	1048.8 (0.16)	--	355.6 (0.02)
w10[2]	0.10 (0.77)	293.8 (0.01)	334.9 (0.02)	253.9 (0.01)	498.9 (0.03)	7531.0 (3.07)	1215.8 (0.20)	150.0 (0.00)	221.7 (0.01)
w11[2]	0.16 (0.52)	456.5 (0.02)	535.1 (0.03)	1138.6 (0.20)	2755.0 (0.48)	6141.8 (1.33)	954.9 (0.13)	--	345.0 (0.01)
w12[2]	0.14 (0.59)	484.3 (0.04)	347.8 (0.02)	526.4 (0.05)	4120.5 (1.44)	1711.2 (0.51)	1268.3 (0.25)	--	242.5 (0.00)
w13[2]	0.13 (0.39)	386.0 (0.02)	659.4 (0.06)	904.5 (0.11)	3311.6 (0.82)	1873.4 (0.48)	693.9 (0.06)	--	254.4 (0.01)
k1[3]	0.10 (0.48)	431.4 (0.03)	393.90 (0.02)	421.9 (0.03)	600.0 (0.03)	5832.8 (1.50)	637.4 (0.10)	--	448.0 (0.02)
k2[3]	0.22 (0.92)	286.0 (0.03)	321.5 (0.02)	522.0 (0.03)	1291.8 (0.19)	11650.6 (2.77)	1844.4 (0.31)	1352.2 (0.16)	502.8 (0.03)
k3[3]	0.20 (0.97)	332.7 (0.02)	471.2 (0.02)	--	760.8 (0.06)	16055.0 (3.40)	1185.1 (0.15)	846.7 (0.11)	482.6 (0.03)
k4[3]	0.09 (0.20)	625.9 (0.08)	576.0 (0.06)	1824.3 (0.52)	626.0 (0.07)	1860.5 (0.24)	675.2 (0.08)	245.0 (0.02)	595.9 (0.04)
k5[3]	0.13 (0.46)	262.5 (0.01)	343.6 (0.03)	275.0 (0.02)	3554.5 (0.90)	2416.0 (0.74)	1363.1 (0.29)	249.0 (0.02)	282.4 (0.02)
w3[3]	0.17 (1.78)	325.0 (0.02)	315.6 (0.01)	714.0 (0.08)	415.5 (0.01)	37750.0 (9.89)	606.7 (0.05)	--	365.8 (0.02)
w4[4]	0.21 (1.19)	410.0 (0.02)	--	84770.0 (0.00)	410.0 (0.04)	602.5 (0.09)	220.0 (0.02)	--	90.0 (0.00)
w6[4]	0.11 (0.41)	380.0 (0.01)	132.5 (0.00)	3597.0 (1.05)	2666.3 (0.36)	983.3 (0.16)	522.1 (0.08)	100.0 (0.00)	308.1 (0.02)
r1[5]	0.16 (1.72)	250.3 (0.02)	280.4 (0.02)	557.9 (0.07)	1410.0 (0.20)	2317.1 (0.47)	22029.2 (7.86)	355.2 (0.02)	320.5 (0.02)
r2[5]	0.07 (0.09)	302.4 (0.02)	417.5 (0.03)	1201.8 (0.19)	831.1 (0.06)	639.4 (0.05)	659.6 (0.07)	1095.2 (0.12)	548.4 (0.03)
r3[5]	0.07 (0.13)	191.0 (0.01)	267.2 (0.02)	496.8 (0.09)	1161.6 (0.13)	1526.0 (0.26)	790.0 (0.12)	510.8 (0.06)	373.1 (0.03)

Appendix 4 Mean minimum distances (± standard error) between patches of different FDPs in 22 study sites and management types: [1]different management, [2] naturalness-promoting management, [3] recently unmanaged, [4] recently unmanaged and former shelterwood logging, [5] long-term unmanaged. Data is given in m, abbreviations of FDPs are explained in Fig. 3.

Study site	Gap	Reg	Ini	erO	mO	laO	Ter	Dis
w1[1]	46.11 (5.87)	44.13 (8.05)	31.99 (5.33)	87.54 (27.68)	24.24 (4.95)	12.08 (0.95)	--	100.23 (43.02)
w2[1]	50.87 (6.48)	83.35 (14.27)	167.59 (51.73)	254.98 (87.88)	--	36.11 (3.30)	--	--
w21[1]	64.29 (7.38)	112.67 (27.02)	213.21 (15.13)	114.45 (43.01)	6.92 (1.53)	20.29 (1.14)	--	233.10 (64.17)
w22[1]	115.58 (14.83)	173.64 (94.69)	--	--	--	40.27 (2.97)	--	104.41
w7[2]	71.36 (9.83)	17.10 (1.49)	37.23 (6.29)	169.35 (45.28)	25.88 (2.66)	9.11 (0.63)	--	64.47 (11.27)
w8[2]	64.13 (11.41)	28.28 (2.19)	219.13 (53.66)	54.38 (9.54)	9.31 (1.26)	12.38 (0.67)	--	89.39 (10.54)
w9[2]	92.00 (17.51)	15.64 (1.28)	25.75 (4.62)	101.59 (17.40)	13.86 (1.59)	11.50 (0.63)	--	178.67 (59.36)
w10[2]	29.95 (3.52)	24.28 (1.81)	51.74 (6.35)	30.96 (2.14)	7.40 (1.05)	15.23 (1.30)	--	49.87 (7.70)
w11[2]	94.37 (14.22)	33.76 (2.65)	71.47 (18.40)	33.53 (11.30)	11.33 (1.67)	20.57 (1.69)	--	92.40 (17.86)
w12[2]	37.62 (4.00)	38.11 (5.36)	63.83 (12.07)	33.53 (2.63)	26.24 (2.56)	20.70 (2.32)	--	279.92 (71.53)
w13[2]	37.74 (6.41)	35.34 (5.83)	51.28 (8.50)	16.93 (2.04)	14.45 (1.14)	21.82 (2.09)	--	113.10 (26.41)
k1[3]	72.60 (33.56)	36.26 (9.43)	57.68 (14.71)	42.02 (7.31)	7.32 (1.01)	13.72 (0.79)	-	99.57 (17.41)
k2[3]	85.91 (18.86)	118.82 (42.59)	209.87 (80.25)	162.81 (43.16)	10.35 (2.06)	12.81 (1.06)	142.29 (33.69)	67.46 (9.94)
k3[3]	133.47 (22.42)	76.15 (16.32)	--	126.57 (34.41)	8.78 (1.48)	15.05 (0.68)	87.47 (14.14)	52.10 (7.95)
k4[3]	30.08 (7.53)	51.43 (13.36)	56.74 (20.58)	51.35 (17.23)	13.91 (2.21)	27.89 (5.09)	204.25 (174.08)	30.24 (7.89)
k5[3]	186.83 (67.19)	67.63 (17.65)	100.09 (8.97)	13.33 (5.10)	9.56 (0.94)	13.93 (2.40)	32.16 (12.09)	37.15 (7.88)
w3[3]	245.44 (70.06)	63.81 (14.71)	81.79 (11.30)	93.38 (15.40)	9.99 (2.00)	18.89 (1.39)	--	49.12 (7.77)
w4[4]	--	--	--	56.67 (9.09)	31.73 (6.24)	55.89 (14.03)	--	--
w6[4]	68.00 (60.10)	18.71 (5.86)	11.82 (1.56)	45.82 (21.47)	16.28 (1.97)	13.37 (1.10)	--	53.71 (12.43)
r1[5]	61.01 (12.43)	47.66 (3.89)	25.13 (1.77)	112.44 (57.44)	49.20 (8.75)	10.72 (2.08)	76.57 (10.67)	35.64 (3.24)
r2[5]	65.65 (10.40)	48.97 (7.65)	20.63 (2.07)	28.02 (6.49)	24.03 (3.07)	24.05 (1.96)	18.52 (3.40)	22.78 (1.58)
r3[5]	46.69 (6.45)	54.98 (10.58)	40.99 (6.72)	17.76 (2.99)	15.48 (2.40)	25.87 (3.82)	26.80 (4.29)	22.23 (2.66)

Appendix 5 Aggregation index R for different FDPs in 22 study sites and management types: [1]different management, [2] naturalness-promoting management, [3] recently unmanaged, [4] recently unmanaged and former shelterwood logging, [5] long-term unmanaged. Abbreviations of FDPs are explained in Fig. 3.

Study site	Gap	Reg	Ini	erO	mO	laO	Ter	Dis
w1[1]	0.94	0.83	0.68	0.95	0.52	0.34	--	1.29
w2[1]	0.92	1.10	1.20	1.64	--	0.81	--	--
w21[1]	1.11	1.35	1.53	0.97	0.06	0.44	--	1.67
w22[1]	1.16	1.23	--	--	--	0.82	--	0.93
w7[2]	1.24	0.50	0.77	1.52	0.61	0.22	--	1.04
w8[2]	1.16	0.69	1.40	1.05	0.16	0.34	--	1.24
w9[2]	1.30	0.47	0.57	1.28	0.38	0.39	--	1.69
w10[2]	0.74	0.77	1.05	0.85	0.12	0.42	--	0.97
w11[2]	1.16	0.84	0.98	0.55	0.19	0.59	--	1.17
w12[2]	0.89	0.72	1.06	0.58	0.63	0.54	--	1.76
w13[2]	0.71	0.69	0.94	0.35	0.37	0.63	--	1.16
k1[3]	1.21	0.90	1.03	0.92	0.14	0.55	--	1.41
k2[3]	1.10	1.42	1.55	1.79	0.14	0.35	1.41	1.20
k3[3]	1.40	0.99	--	1.38	0.10	0.46	1.07	0.91
k4[3]	0.67	1.08	1.15	0.88	0.34	0.84	2.22	0.77
k5[3]	2.45	1.33	1.43	0.25	0.80	0.45	0.80	1.11
w3[3]	1.86	0.98	0.98	0.96	0.08	0.63	--	0.87
w4[4]	--	--	--	1.11	0.92	1.14	--	--
w6[4]	0.57	0.18	0.26	0.63	0.45	0.51	--	1.04
r1[5]	1.00	1.03	0.65	0.59	0.69	0.12	1.07	0.87
r2[5]	1.21	1.11	0.51	0.58	0.69	0.72	0.52	0.69
r3[5]	1.16	1.27	0.97	0.49	0.42	0.73	0.71	0.75

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Impact of naturalness-promoting forest management on forest structure

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Abstract:	Context: Forest development phases (FDPs) divide the forest life cycle into different periods. Therewith, a forest stand can be divided into differently structured FDP patches representing developmental steps. Aims: This study emphasises the impact of naturalness-promoting forest management on FDP proportions and patchiness in comparison with recently unmanaged (for 20-35 years) and long-term unmanaged (for 65 and more than 100 years) forests. Methods: In 2002 and 2012/2013, we investigated FDPs in eight lowland beech forests (Fagus sylvatica L.; 12-43 ha) in north-eastern Germany. FDP patches were recorded according to a dichotomous decision tree of variables - diameter at breast height, canopy cover, amount of deadwood, regeneration, and tree height - related to forest life cycle. Results: Naturalness-promoting management showed the same development of FDP proportions as recently unmanaged stands, including a development of FDPs into subsequent FDPs. In long-term unmanaged sites, FDP proportions remained similar within the observed decade. Analysis of transition dynamics revealed that naturalness-promoting management has a positive effect on FDP diversity and horizontal structural heterogeneity. Conclusion: A decade of naturalness-promoting management resulted in a more fine-grained FDP distribution with more even proportions and smaller FDP patches. This kind of management supports small-scale heterogeneity and structural complexity of harvested forests.
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Impact of naturalness-promoting forest management on forest structure

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KEY MESSAGE

Analysis of the distribution of forest development phases (FDPs) - periods of the forest life cycle - is a comprehensive way to investigate forest structure as indirect biodiversity indicator. Management integrating nature conservation aspects promotes a higher FDP richness and results in decreasing patch sizes comparable to trends of recently unmanaged stands.

ABSTRACT

Context: Forest development phases (FDPs) divide the forest life cycle into different periods. Therewith, a forest stand can be divided into differently structured FDP patches representing developmental steps.

Aims: This study emphasises the impact of naturalness-promoting forest management on FDP proportions and patchiness in comparison with recently unmanaged (for 20-35 years) and long-term unmanaged (for 65 and more than 100 years) forests.

Methods: In 2002 and 2012/2013, we investigated FDPs in eight lowland beech forests (*Fagus sylvatica* L.; 12-43 ha) in north-eastern Germany. FDP patches were recorded according to a dichotomous decision tree of variables – diameter at breast height, canopy cover, amount of deadwood, regeneration, and tree height – related to forest life cycle.

Results: Naturalness-promoting management showed the same development of FDP proportions as recently unmanaged stands, including a development of FDPs into subsequent FDPs. In long-term unmanaged sites, FDP proportions remained similar within the observed decade. Analysis of transition dynamics revealed that naturalness-promoting management has a positive effect on FDP diversity and horizontal structural heterogeneity.

Conclusion: A decade of naturalness-promoting management resulted in a more fine-grained FDP distribution with more even proportions and smaller FDP patches. This kind of management supports small-scale heterogeneity and structural complexity of harvested forests.

INTRODUCTION

The natural structure of European beech (*Fagus sylvatica* L.) forests is characterised by a fine-scaled mosaic of diverse patches representing different forest development phases (FDPs) (e.g. Bobiec et al. 2000; Emborg et al. 2000; Korpel 1995; Oldemann 1990; Remmert 1991; Watt 1947; Winter and Brambach 2011). Each patch follows its own life cycle without being synchronised with neighbouring patches (Wissel 1992); however, patches have an influence on their neighbours e.g. by trees falling into a neighbouring patch or by shading a neighbouring patch. FDPs divide the forest life cycle into different periods based on a defined combination of several structural parameters such as canopy cover, diameter at breast height (DBH), tree height, amount of deadwood, and regeneration cover (e.g. Tabaku 2000).

Most beech stands in Central Europe are even aged; there are only a few beech forests that are unaffected by man (Tabaku 2000). With 25% of its global range, Germany hosts the core area of the European beech forest occurrence (Bohn and Weber 2000). Thus, Germany has a particular responsibility and opportunity to integrate biodiversity conservation into forest use (Flade et al. 2004; Knapp 2007; Winter et al. 2013). The Convention on Biological Diversity (CBD 1992), the Habitats Directive (92/43/EEC) and the biodiversity strategy of the Commission of the European Communities (2003) all highlight the importance of the protection and sustainable use of forests and their biodiversity.

Naturalness (defined as “similarity of a current ecosystem state to its natural state”; cited from Winter 2012), is an important characteristic for the preservation of global biodiversity (Reif and Walentowski 2008; Winter 2012). As forest management affects the forest biodiversity (e.g. overview Paillet et al. 2010), nature conservation is an important management objective. Forest management should promote a near-natural stand structure (e.g. Christensen and Emborg 1996; Flade et al. 2004; Kraus and Krumm 2013; Lindenmayer et al. 2006; Rosenvald and Lõhmus 2008; Winter et al. 2005) and should seek to achieve a more natural FDP patch distribution (Drößler and Meyer 2006; Rugani et al. 2013; Tabaku 2000; Zenner et al. 2015) – in order to provide the range of habitats required by forest inhabiting species (Begehold et al. 2015; Flade et al. 2004; Regnery et al. 2013; Suchan and Baritz 2000; Winter 2005; Winter et al. 2005).

Several studies confirm that forest biodiversity is connected to the pattern and distribution of FDPs (Müller et al. 2005; Winter and Brambach, 2011; Winter et al. 2005; Winter and Möller 2008), but knowledge of how FDP composition and the spatial distribution of FDPs changes over time in natural forests is scarce (Král et al. 2014); even less is known about temporal FDP dynamics in managed forests. Such knowledge would be important in determining the impact of naturalness-promoting management on forest structure.

In this study, we compare the FDP patch dynamics in beech stands with naturalness-promoting management and in (recently) unmanaged beech stands. We analyse changes in FDP proportions, development of patchiness and transition processes over a decade in order to investigate the influence of naturalness-promoting forest management on forest structure. We hypothesise that under naturalness-promoting management: (i) a wider distribution of FDPs can be achieved and become more similar to the FDP distribution in unmanaged forests; (ii) similar transition proportions to those in unmanaged forests can be supported; and (iii) patch size will decrease due to the sustainable harvesting regime.

METHODS

Study area

The study area is comprised of eight beech-dominated sites located in north-eastern Germany (Table 1). Three of the sites have been continuously managed, but within the last decade management has focused on promoting naturalness following eight silvicultural criteria: single tree or small tree group cutting; a heterogeneous stand structure; thresholds for deadwood amount and dimensions; conservation of, and thresholds for, microhabitats; natural tree regeneration; and diameter thresholds for tree harvesting (Appendix 1). The other sites have been left unmanaged for different periods: on two sites there has been no management since 1998; on one site there has been no management since 1990; on one site there has been no management for over 60 years; and on another site there has been no management for at least 100 years.

All study sites are mature forests with trees of at least 120 years (with a maximum of 400 years) and grow in mesotrophic soil conditions (Kopp and Schwanecke 1994). The sites are located between 52.8 – 53.3°N and 13.0 – 13.9°E. Climatic conditions are similar for all sites (continental according to Article 1c of the Commission of the European Communities 2003): altitude varies between 43 and 130 m above sea level; mean annual precipitation (1981-2010) ranged from 519 to 629 mm per year; and mean annual temperature (1981-2010) ranged from 8.4 to 8.9°C for (DWD 2013). Five study sites had an area of about 30-40 ha, one long-term unmanaged site was 13.6 ha, and two of the recently unmanaged sites that were previously subjected to a shelterwood logging regime (35 years ago) had areas of 11.4 ha and 17.1 ha (Table 1).

FDP mapping

FDPs were investigated in 2002 and 2012/2013 using a method developed by Tabaku (2000), and simplified for use in the field by Winter (2005). FDP mapping depicts the spatial characterization of a forest stand including the exact position and expansion of each FDP patch. All homogeneous FDP patches with a minimum area of at least 196 m^2 (which is the maximum extension of an old single tree with a wide crown working as an ecological unit) were recorded following a dichotomous decision tree, integrating different structural parameters (see Winter and Brambach 2011: Fig. 4). Patches were identified in the field according to the dynamic frame method described in detail in Begehold (2016): For the identification of the patches, the following dichotomous decisions were required: 1) the area of tree canopy cover was more or less that 30 % or the area of regeneration cover was more or less than 50 %; 2) Standing and lying deadwood was measured (length, diameter) and the total amount was determined as more or less than 30 % of the total wood volume within the patch; 3) The measured DBH was > 20 cm, 40 cm or 60 cm. We used GPS with an accuracy of ± 1 meter (corrected by differential GPS correction data). The field maps were transferred to the ESRI geographical information system (ArcGIS 9.3.1). Swampy areas emerging from kettle holes formed by retreating glaciers are typical elements of beech forests in the study region and were mapped in addition to the FDPs to ensure consistency in the study area between the two mapping periods.

FDP proportion analyses

FDP proportions (%) per study site and recording period were summarised as compositional data by a non-metric multidimensional scaling (NMDS) using Aitchison dissimilarity in order to account for their compositional nature. Stress values were below 0.15 in all cases. The concordance of FDP composition in 2002 and 2012/2013 was determined using a Procrustean superimposition approach

(Gower 1971). The superimposition makes it possible to determine the relative change in FDP composition for each site. To estimate Procrustes correlation *r* and the statistical significance of the Procrustean fit, the permutation procedure PROTEST (Jackson 1995) was used with 9999 permutations. Residuals were then averaged according to management type and time since abandonment.

FDP transition

To analyse changes in FDPs within the ten-year time period, we compared FDP patch identity from 2002 with patch identity in 2012/2013. The total investigated area of all patches was 254.3 ha (n =1,081 in 2002). We then calculated the area of each FDP that had remained unchanged (persistence) or had changed into a different FDP (transition). For these analyses, we used data from seven study sites; one recently unmanaged site (w6) had to be excluded due to some topographical coordinate problems during the first mapping. However, we took a second record in 2012 for this study site in order to take it into account for the FDP proportion and patch size analyses.

We calculated transition diversity (diversity of different FDPs one certain FDP converts to from 2002 to 2012) using Shannon index (Shannon 1948):

$H = -\sum_{i=1}^{n} p_i \cdot \ln p_i$ where p_i is the proportion of the *i*-th FDP to which a FDP is transformed.

For reliable comparisons between study sites in relation to FDP transition, we verified that the probability of a transformation into a subsequent FDP was similar across all study sites. To control for different probabilities of FDP transition depending on the duration of each particular phase and to ensure that the results were not biased by this, we tested whether the transition probability was comparable across study sites. Therefore, we took tree dimension data like DBH and tree height from records in 2002 (Winter et al. 2003; a forerunner project) and calculated the theoretical growth in ten years to compare the proportions of reaching the subsequent FDP within the life cycle.

Patch size

We tested whether median patch size differs between management types using Wilcoxon Rank Sum tests. To analyse the effect of management or time since abandonment on changing patch size of the single FDPs within the last decade, we compared the median patch sizes for each FDP and management type and calculated the 95 % confidence interval.

Patch sizes were calculated using ArcGIS 9.3.1 (ESRI, Redlands, CA). All other calculations and graphics were computed in R (R Core Team 2012) using the packages “vegan” (Oksanen et al. 2013), and “compositions” (v.d. Boogaart et al. 2013).

RESULTS

Changes in FDP proportions

In study sites managed to promote naturalness and in recently unmanaged study sites, FDP proportions developed in a similar way (Fig. 2a). Both showed the strongest increase in the proportion of late optimum phases combined with the greatest decrease in the proportion of the mid-optimum phase (Fig. 2a, Appendix 4). The change in the proportion of the disintegration phase was highest in recently unmanaged study sites. FDP compositions are rather similar (r = 0.8764, Fig. 2b) in the consecutive records across all study sites. Changes in FDP proportions indicated by average residuals are highest and showed the largest range in study sites subjected to naturalness-promoting management (Fig. 2c).

The greatest changes among the proportions of the different FDPs were found for the late optimum phase (increase) in all management types except for the long-term unmanaged sites (here, the proportion of the initial phase increased the most, Fig. 2a). The proportion of the mid-optimum phase decreased in all management types; proportions of gaps, regeneration, terminal and disintegration phases did not change or changed only slightly in all management types (Fig. 2a).

FDPs such as the terminal and disintegration phases are still less frequent in managed compared to unmanaged study sites.

FDP persistence and transition

FDP transition clearly differed between the management types. Under naturalness-promoting management, on average, 59 % of the study area (38-77 %) transformed into a different FDP during the 10-year period. In the two recently unmanaged sites, the amount varied between 20 % and 37 %. In study site r1 (unmanaged for > 60 years), 23 % of the area changed its FDP, whereas 38 % of the area changed its FDP in the long-term unmanaged study site (for > 100 years, r3).

The proportion of FDP transition (Fig. 3) illustrates the differences between the three management types with regard to several FDPs. Transition proportion of individual FDP patches that did not involve a transformation into the subsequent FDP also occurred. The changes from each of the 2002 FDPs were:

(1) Gaps: Under naturalness-promoting management and in long-term unmanaged study sites, transition diversity of gaps was high (Fig. 4a) and most parts remained as gaps or developed into the regeneration phase, whereas smaller proportions changed into optimum phases (Fig. 3a). In recently unmanaged study sites, gaps also remained or changed into the initial phase or into the late optimum phase.

(2) Regeneration: In all management types, a similar proportion of former regeneration phase remained or changed mainly into the subsequent initial phase (Fig. 3b).

(3) Initial phase: The former initial phase mainly remained but also developed into the subsequent early optimum phase (naturalness-promoting management) or into the mid- or late optimum phases (naturalness-promoting management and recently unmanaged study sites, Fig. 3c).

(4) Optimum phases: The former early and late optimum phases changed to a similar amount in all management types (Fig. 3d-f). About the half of the early optimum phase (48-59 %) and the majority of late optimum phase (75-98 %) persisted, whereas a small proportion developed into regeneration phase (naturalness-promoting management) or late optimum phase, disintegration phase (with the highest transition diversity in long-term unmanaged sites).

An average of 55 % (38-66%) of the former mid-optimum phase changed under naturalness-promoting management; 39 % (24-53 %) grew up to the late optimum phase (Fig. 3e) 17 % changed in other FDPs with the highest transition diversity. With 33 % on average, a lower proportion of the mid-optimum phase in unmanaged study sites underwent transition (24% in recently unmanaged and 41 % in long-term unmanaged sites).

(5) Terminal and disintegration phase: A high proportion – 79-99 % (Fig. 3g, h and Fig. 4 g, h) – of the terminal and disintegration phases persisted, while the latter changed in small proportions

into other FDPs across all management types. Transition diversity was highest in long-term unmanaged study sites.

FDP patch size

The average patch size for all eight FDPs together has mainly decreased between 2002 and 2012/2013 across the different management types (Table 2). However, median patch sizes of single FDPs varied strongly and changed distinctively across the management types over the decade (Fig. 5).

Under naturalness-promoting management, the median patch size across all FDPs decreased ($p < 0.001$, Wilcoxon Rank Sum test). The median patch size of single FDPs also decreased within the 10-year period (Fig. 5) for all FDPs except the late optimum phase (Fig. 5f). These changes are significant except for the initial and disintegration phases. The median patch size of the mid-optimum phase was strongly reduced towards values comparable to unmanaged study sites (Fig. 5e).

In unmanaged study sites, patch size did not significantly differ between 2002 and 2012 ($p = 0.94$ for recently unmanaged, $p = 0.187$ for long-term unmanaged study sites).

Generally, the patch sizes in both recording periods were usually smaller for gaps, regeneration, terminal and disintegration phases than for the optimum phases (Table 2; Fig. 5). In unmanaged study sites, disintegration phase patches varied most in terms of patch size (from 0.01 ha to 0.2 ha; Fig. 5h).

DISCUSSION

Changes under naturalness-promoting management

Our results show that after a decade, naturalness-promoting management created an FDP composition that is moving towards that of the recently and long-term unmanaged sites. On sites under naturalness-promoting management there was a greater richness of FDPs after ten years, and the transition diversities between naturalness-promoting management sites and unmanaged sites were similar. The changes in FDP proportions and transition were also similar to unmanaged study sites (Figs. 2a, 3, 4, Tab. 2) and the decreased patch size became more similar to a small-scale mosaic as in long-term unmanaged stands, indicating a more natural development according to the changed management criteria (Fig. 5, Appendix 1). In consequence, naturalness-promoting management enhanced the development of FDPs such as disintegration phases (patch number increased) that are important, for instance, for maintaining forest biodiversity (e.g. Fichtner et al. 2014; Möller 2005; Müller et al. 2005; Winter and Möller 2008). At the same time, forest resources were available for wood use. The disintegration phase can be developed from different FDPs (Fig. 3) and accomplished by maintaining deadwood and allowing natural ageing of at least 5 trees with a DBH ≥ 40 cm per hectare (Appendix 1). The results indicate that it is possible to detect changes in silviculture over a short period: decreasing mean patch size, a high transition percentage from the mid-optimum phase (a dominant phase in our managed forests), and a high transition diversity developed under naturalness-promoting management.

It should be noted that all study sites were mature with a stand age of at least 120 years. For younger stands, the impact of a naturalness-promoting management may be different and remains to be studied.

Changes in unmanaged stands

The differences in FDP composition changes within a decade in the two long-term unmanaged study sites indicate that 60 years without management in one of the study sites was not a long enough time period for it to develop into a state comparable to a forest unmanaged for 100 years or even to primeval forests (Drößler and Meyer 2006). Long-term unmanaged stands achieve a perpetually balanced dynamic with fluctuations in FDP proportions over time (Rademacher et al. 2004) as long as there are no large-scale disturbances. Occasional intermediate disturbances are also part of the natural disturbance regime in beech forests and have been confirmed by several studies (e.g. Hobi et al. 2015; Zenner et al. 2015). Phases such as the terminal and disintegration phases were found less frequently (16-42 patches) in managed compared to unmanaged study sites (69-103 patches) (see also Bobiec et al. 2000), even though the abundance of these FDPs increased slightly in our study sites (Appendix 3). For long-term unmanaged study sites, our results confirm findings from studies of forest reserves that have been unmanaged for more than 60 years (Heiri et al. 2009; Winter 2005) and of primeval beech forests (Meyer et al. 2003), which report that FDP proportions are quite similar and that patch sizes are small across nearly all FDPs due to the presence of all FDPs. With our results, we also confirmed that in recently unmanaged study sites, natural development was apparent, but development of a fine-scaled FDP structure with small patches and a complete FDP set as observed in long-term unmanaged study sites had not yet been reached (Heiri et al. 2009), even though larger homogeneous patches are also a feature of natural stands (Leibundgut 1982). Casual changes due to natural disturbances in unmanaged stands have to be considered separately from the rather regular impact as a consequence of human interventions.

Development of FDP patches and transition

In line with Král et al. (2014), we found that the proportion of the disintegration phase increases with time since the last harvest (compare Fig. 2a), and that gaps can become smaller, consistent with an area that would open up following the simultaneous death and treefall of 1-3 canopy trees (Kenderes et al. 2009).

Also in line with Král et al. (2013; 2014) we found that the mean patch size of each FDP varies significantly. In addition, different mean patch sizes among FDPs in 22 study sites investigated in 2012/13 might also apply for the different management types (Begehold et al. 2016). The changes in patch size may be caused by different processes and can be related to transition which differs from the chronological FDP development (gap → regeneration → growth → optimum → decay → gap):

- *Lateral crown expansion* (Christensen et al. 2007) can lead to increased patch size as in recently unmanaged study sites, where the canopy of the gap surrounding trees compensates or closes the gap caused by a single tree fall. In managed study sites canopy gaps as a result of single tree cutting can be closed the same way. As a consequence, patches of gaps or the regeneration phase can shrink within a short period of time (this was also discussed by Knapp and Jeschke 1991; Splechtna and Gratzer 2005) or become optimum phases.
- *Canopy replacement* (Christensen et al. 2007) from the lower canopy as takeover from young trees creates smaller patch sizes; e.g. transition from former optimum or terminal phase patches (into gap, regeneration phase, initial phase or other optimum phases, see also Fig. 3d-g) is often the result of canopy replacements when regeneration or other FDPs are already present in the understorey. In consequence, dynamics of the sub-canopy trees (as well as dynamics in the overstorey) play an important role in FDP dynamics of the tree layer (Christensen et al. 2007; Král et al. 2014; Manabe et al. 2009).

- *Growth* and thereby increasing DBH of trees close to the defined FDP threshold that distinguishes between two FDPs can vary patch sizes. In recently unmanaged study sites, for instance, late optimum phase patches often develop from the mid-optimum phase due to DBH extension of numerous trees close to the threshold (that would partly be harvested in managed forests). Otherwise, natural growth of the mid-optimum into the late optimum phase enlarges the patch size of the latter (Fig. 5f). Paluch (2007) assumes that structural patch diversification may depend more on resistance of large canopy trees – as in the late optimum phase, for instance – against disturbances than on competition between them.
- *Local disturbances* such as caused by small windthrow or treefall of a few trees can create smaller patches or lead to small inclusions in the stand matrix built by the disintegration phase (Fig. 3e,f; see also Král et al. 2013, 2014). The emergence of tree regeneration at former gaps or breakdown patches can lead to smaller patches: When regeneration occurs, depending on light conditions in the centre or at the margins of the patch, it can split the breakdown patch into two or more smaller disintegration and regeneration patches (e.g. in our long-term unmanaged sites). In contrast, larger patches result from the fact that disintegration phase patches can develop into optimum, regeneration or initial phases as a result of decomposition, so the deadwood amount decreased under the threshold of 30 % (compare to Tab. 1). Small optimum phase patches can be included in the surrounding regeneration or initial phases caused by decay due to sunburn or windthrow as observed in recently unmanaged study sites (Figs. 3d, 5c).
- *Management* can change FDP patches into patches of previous FDPs (Fig 3), which can increase patch size by harvesting single trees or tree groups; or can decrease patch sizes by reaching the surrounding FDP while harvesting.

From our results, it seems that naturalness-promoting management enhances FDP diversity and the development of FDPs such as late optimum phase, terminal and disintegration phase. The development of one FDP patch does not necessarily follow the chronological FDP order (gap → regeneration → growth → optimum → decay → gap), and thus patches can develop into a FDP different to the chronological order. In light of this, we propose a more complete picture of the forest life cycle for beech forests (Fig. 6), which considers natural and forest management impacts.

CONCLUSION

Our results show that forest structure connected to FDPs can be approached towards long-term unmanaged stands at least partially in managed forests where a naturalness-promoting silviculture concept based on nature conservation criteria is applied. With this approach we were able to confirm that integrated approaches are practicable for forest management that applies multicriterial use of forests such as wood use for economics and wood use for biodiversity.

In conclusion, forest management can be evaluated using FDP records. FDPs can be used as a tool to detect relevant differences within a certain time period. As such, they could be used for forest monitoring, especially for the evaluation of the conservation status of Natura 2000 forest habitats (Habitats Directive 92/43/EEC), because FDPs are a meaningful variable for describing forest dynamics. They describe the complex habitat conditions and provide more biodiversity relevant information than single tree structure variables such as, for instance, the DBH distribution of a forest stand. On the basis of our results, we propose a broad integration of the FDP approach in forest inventory schemes such as the national forest inventory, the federal state and local forest inventories, as well as in nature conservation monitoring.

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TABLES

Table 1 Study sites, sizes, management history and -types.

Study site	Size [ha]	Management type before 2002	Total stock volume 2002 [m^3/ha]	wood harvested 1992-2002 [m^3/ha]	Number of cuttings 1992-2002	Management type between 2002 and 2013	wood harvested 2002-2012 [m^3/ha]	Number of cuttings 2002-2012	Time since management abandonment
w9	40.2	management without nature conservation focus	482.4	[no data]	[no data]	Naturalness-promoting management	126.4	3	--
w10	30.4	management without nature conservation focus	407.8	54.9	4	Naturalness-promoting management	244.0	3	--
w12	40.3	management without nature conservation focus	327.2	55.6	4	Naturalness-promoting management	59.0	1	--
w4	11.4	management without nature conservation focus (former shelterwood logging)	114.6	32.4	3	Recently unmanaged	0	0	15 years

w6	17.1	management without nature conservation focus (former shelterwood logging)	260.9	27.1	1	Recently unmanaged	0	0	15 years
k2	36.5	management without nature conservation focus	650.8	0	0	Recently unmanaged	0	0	25 years
r1	43.1	Long-term unmanaged	695.8	0	0	Long-term unmanaged	0	0	>60 years
r3	13.6	Long-term unmanaged	789.2	0	0	Long-term unmanaged	0	0	>100 years

Table 2 Mean patch sizes ± sd (and patch numbers) of the single FDPs across all study sites in 2002 and 2012/2013.

FDP	Mean patch size 2002 [m^2]	Patch number 2002	Mean patch size 2012/2013 [m^2]	Patch number 2012/13
Gap	0.046 ± 0.07	223	0.038 ± 0.03	193
Regeneration phase	0.065 ± 0.06	228	0.054 ± 0.06	288
Initial phase	0.414 ± 1.91	96	0.121 ± 0.48	226
Early optimum phase	0.177 ± 0.44	111	0.156 ± 0.56	167
Mid-optimum phase	0.677 ± 3.96	205	0.500 ± 2.89	273
Late optimum phase	0.313 ± 2.62	100	0.139 ± 0.85	424
Terminal phase	0.065 ± 0.10	38	0.078 ± 0.10	56
Disintegration phase	0.037 ± 0.03	97	0.039 ± 0.03	191
Swamps	0.09 ± 0.07	27	0.114 ± 0.13	37
All	0.229 ± 1.92	1,125	0.151 ± 1.16	1,855

FIGURES

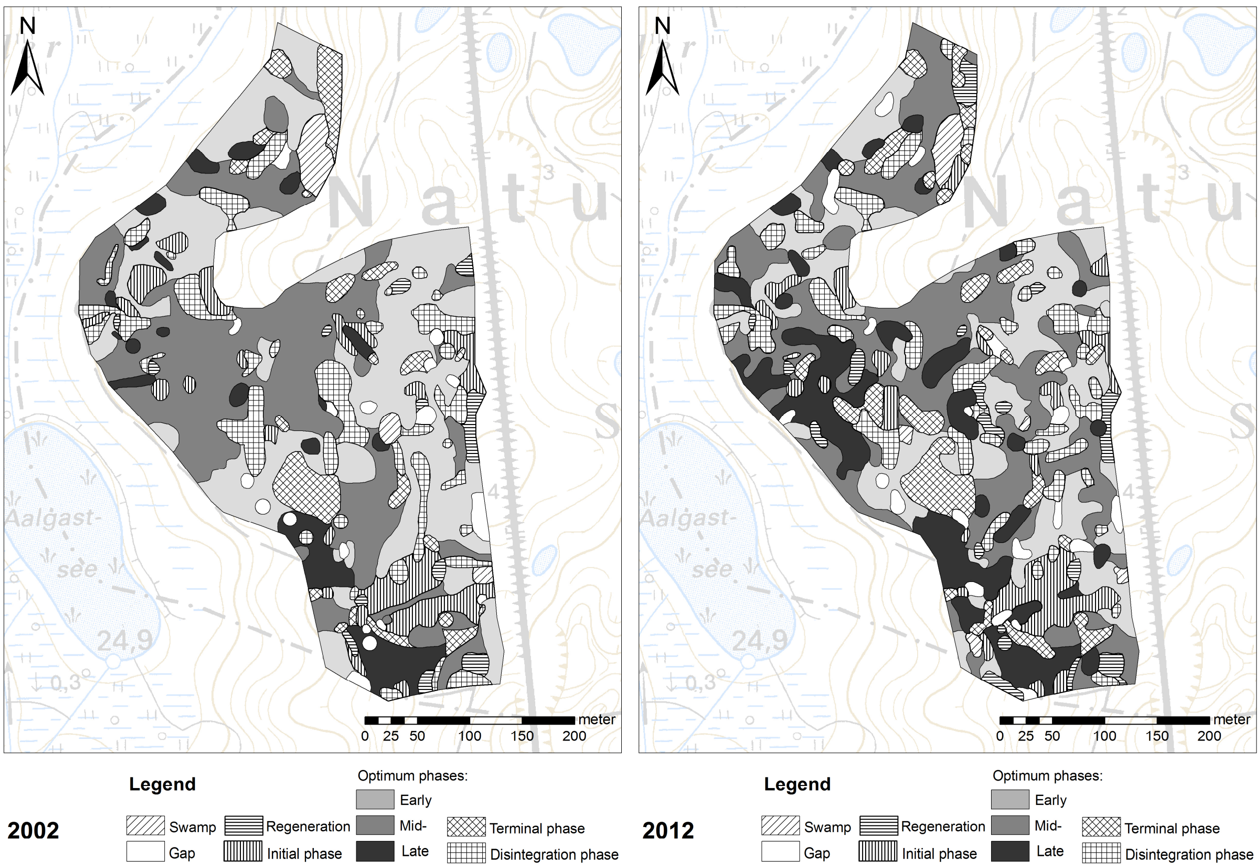


Fig. 1 FDP maps of study site r3 in 2002 (left) and 2012 (right). FDPs were determined directly in the field.

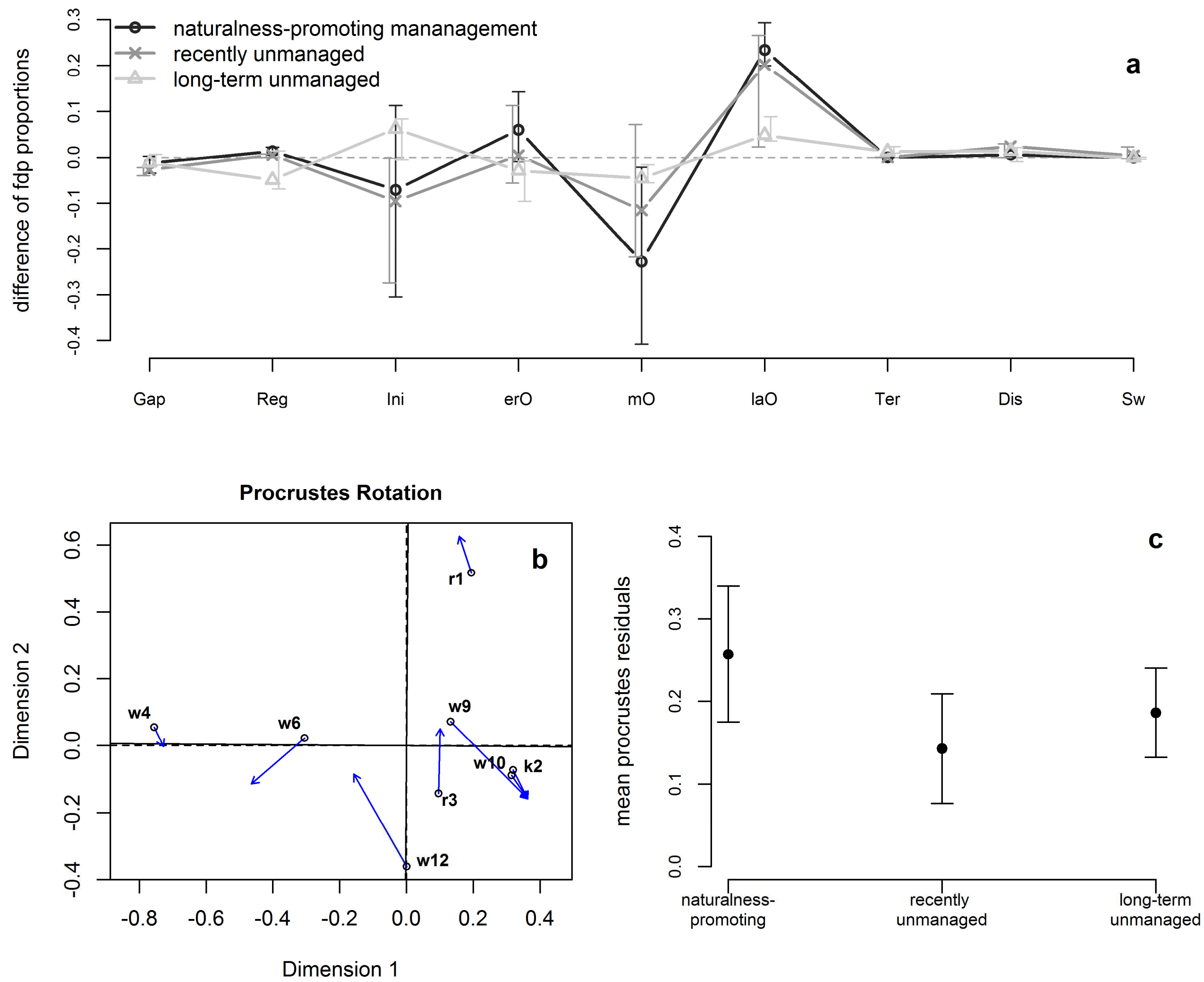


Fig. 2 Relative differences in FDP proportions after a decade with respect to FDP proportions in 2002 (1a, a value of 0.0 indicates no difference, negative values indicate a decrease, positive values indicate an increase in the FDP proportion) and Procrustes superimposition plot (r = 0.8764, p < 0.001, 1b) for the first two dimensions with Procrustes residuals (means across management types with standard error, 1c). w4 and w6 represent former shelterwood loggings, abandoned since 1998, k2 belongs to the recently unmanaged (since 1990) type, w9, w10, w12 are subjected to naturalness-promoting management and r1 and r3 represent long-term unmanaged study sites (for more than 60 and more than 110 years respectively). Reg = Regeneration phase, Ini = Initial phase, erO = Early optimum phase, mO = Mid-optimum phase, laO = Late optimum phase, Ter = Terminal phase, Dis = Disintegration phase, Sw = Swamps. For exact values of FDP proportions in 2002 and 2012/13 see Appendix 4.

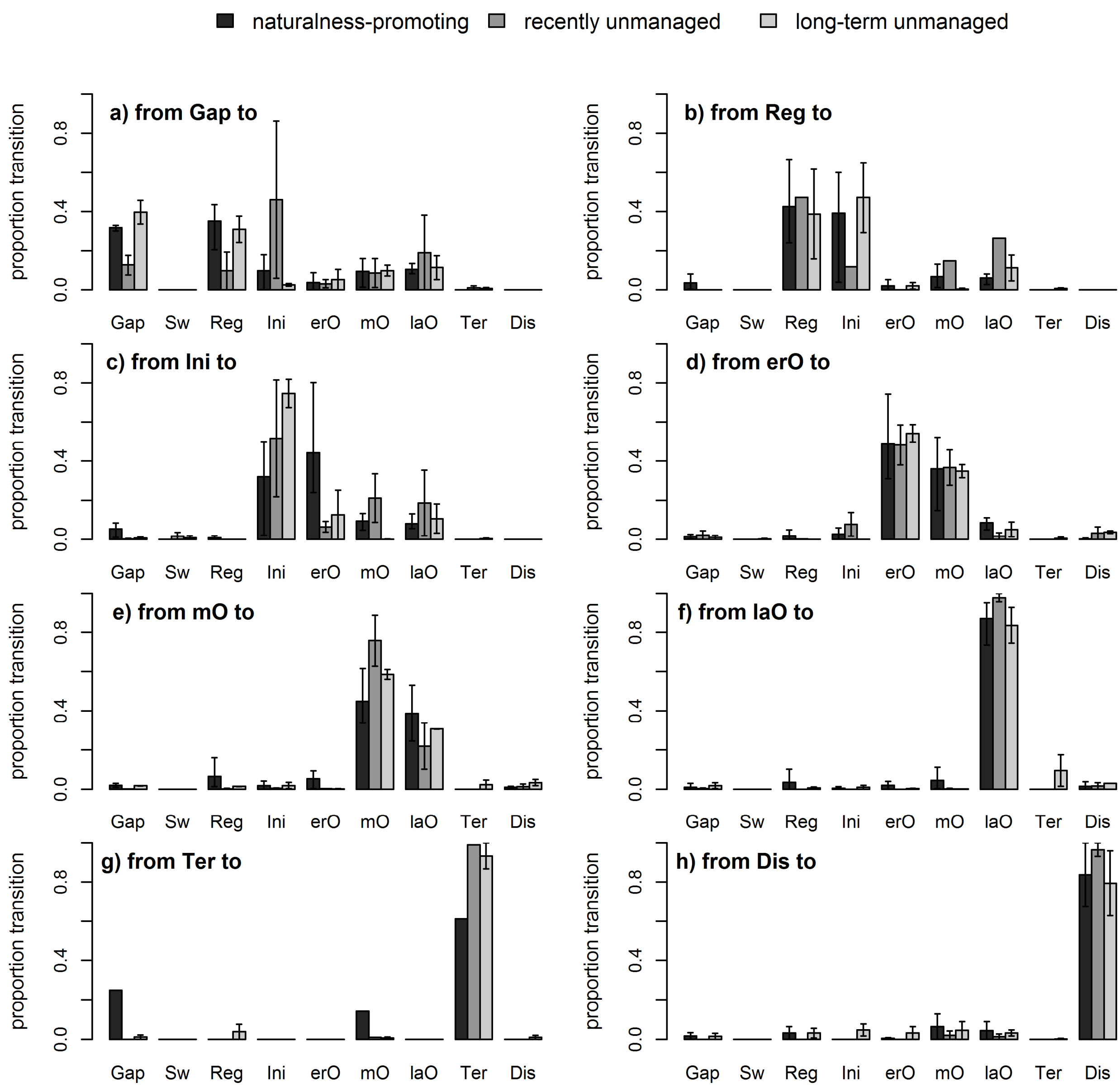


Fig. 3 FDP transition in managed and unmanaged beech forest sites within a time step of ten years. Each figure (3a-h) represents the relative proportions of a single FDP either transforming into a different FDP or remaining unchanged. Error bars represent ranges across study sites. 3a: gap (total area of all 2002 patches = 11.4 ha), 3b: regeneration phase (Reg, 15.2 ha), 3c: initial phase (Ini, 27.9 ha), 3d: early optimum phase (erO, 23.6 ha), 3e: mid-optimum phase (mO, 135.8 ha) and 3f: late optimum phase patches (laO, 33.1 ha), 3g: terminal phase (Ter, 2.4 ha) and 3h: disintegration phase (Dis, 3.6 ha).

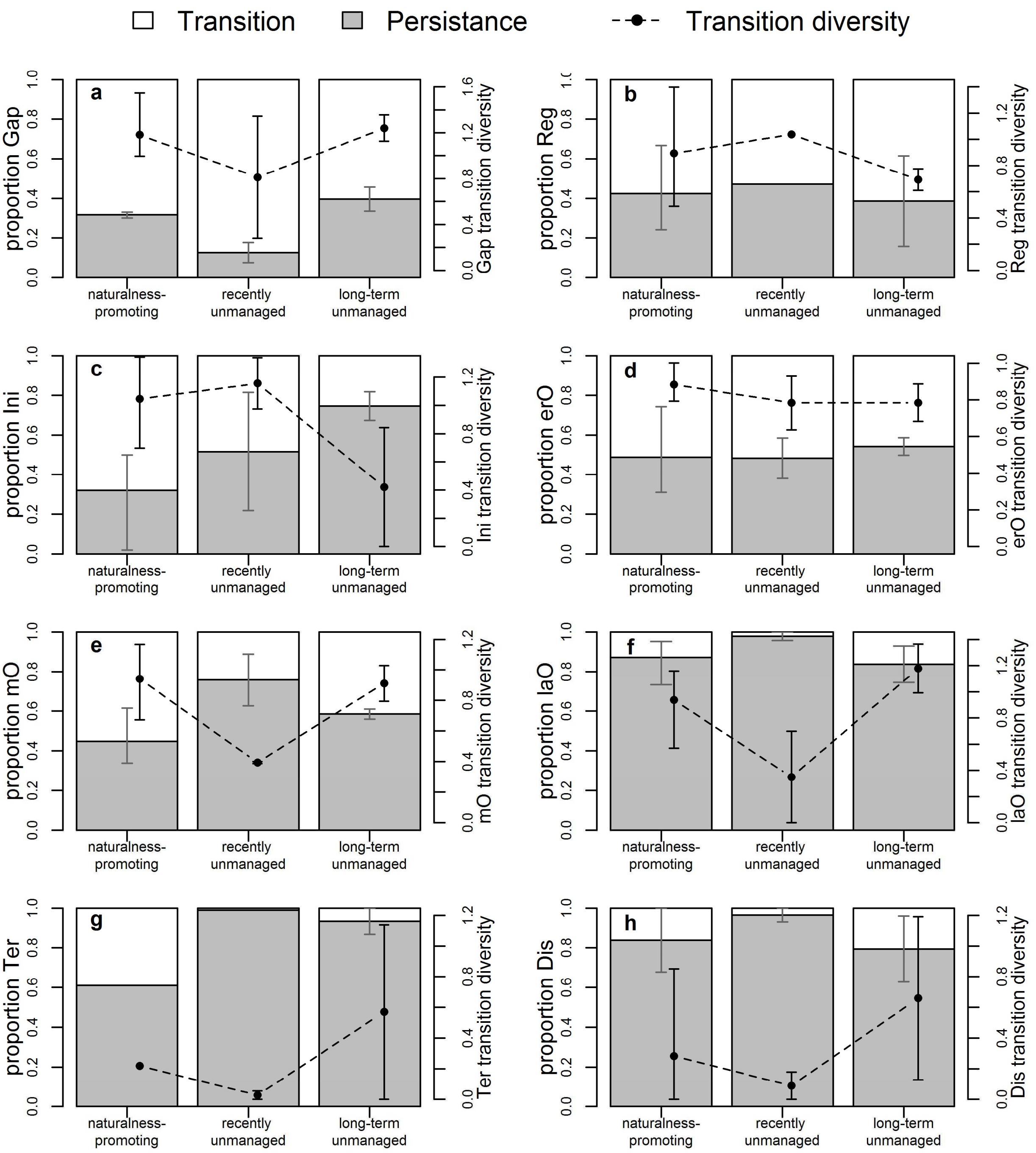


Fig. 4 Persistence and transition diversity of FDPs in managed and unmanaged beech forest sites over ten years. Grey bars represent relative proportions of persisting FDPs, i.e. the percentage of patch area that is assigned to the same FDP as in the earlier recording. White bars represent the percentage of total patch area that transformed into a different FDP compared to the earlier recording. The points represent the transition diversity of the patches that transformed into a different FDP. Further explanations are found in the text. Error bars represent ranges across study sites. 4a: gaps, 4b: regeneration phase, 4c: initial phase, 4d: early, 4e: mid- and 4f: late optimum phase, 4g: terminal phase and 4h: disintegration phase. Abbreviations and sample size are the same as in Fig. 3.

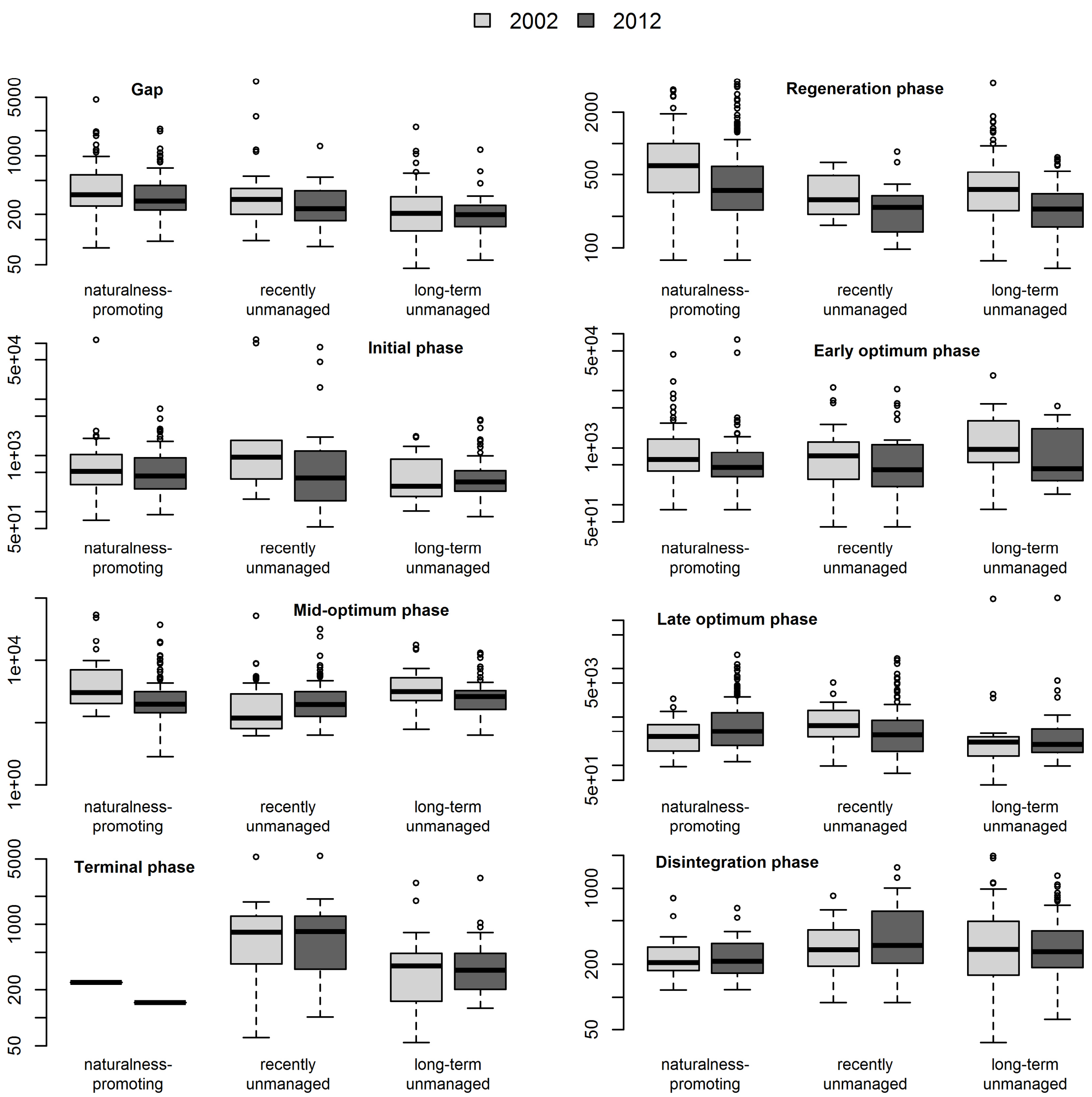


Fig. 5 FDP patch sizes (log scale) in lowland beech forests for different management types and investigation periods. Boxes represent 50 % of the patches (the bottom and top of the box symbolise the first and third quartile with the median inside the box. The whisker thresholds show the minimum and maximum of the distribution, but not more than 1.5-times the interquartile range. Outliers are shown as single points. Area is given in m².

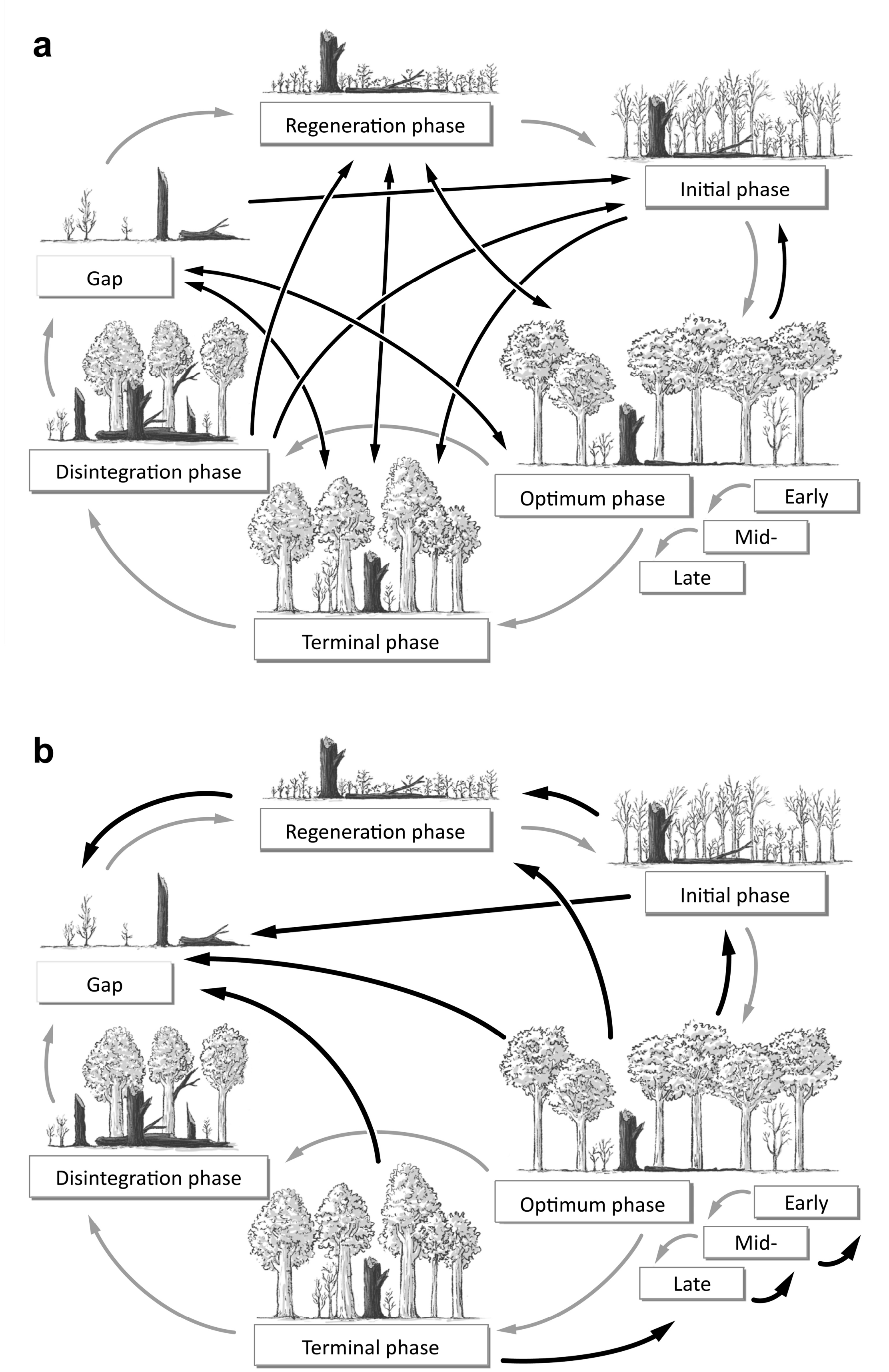


Fig. 6 Forest life cycle in beech forests completed by additional natural and forestry processes. 5a: Further natural processes (black arrows) complete the simplified model (grey arrows). 5b: The simplified model of the forest life cycle (grey arrows) completed by the influence of forest use (black arrows). The three optimum phases only differ in terms of the tree size (Appendix 2).

SUPPLEMENTARY MATERIAL to

Impact of naturalness-promoting forest management on forest structure

Heike BEGEHOLD, Michael RZANNY, Susanne WINTER

Appendix 1 Silviculture concept for naturalness-promoting management cited from Begehold et al., 2016. For further explanations see Winter et al., 2003; Flade et al., 2004.

1.	Silvicultural methods that result in simple and largely homogeneous stand structures, such as shelterwood logging and clearcuts, are not applied. Management units are smaller than one hectare to allow for a heterogeneous stand structure. Gaps are encouraged and not filled by artificial regeneration. The forest is, or will be, multilayered and diversely structured.
2.	Five old trees per hectare (>40 cm DBH) are marked as habitat trees to let them develop microhabitats (Winter and Möller, 2008) with natural ageing processes.
3.	A deadwood amount of at least 30 m^3 per hectare of standing and lying deadwood is provided in different dimensions. In conservation areas a deadwood amount of 50 m^3 per hectare.
4.	To preserve natural structures with habitat functions such as trees with broken crowns or broken trunks, trunks with lightning scars, trunk cavities, or bark pockets. At least 10 of 20 different microhabitat types as defined by Winter and Möller (2008) are present per hectare.
5.	The cutting threshold (trunk target dimension) should be at least 65 cm DBH. Trees should be present with trunk diameters which are successively greater than 65cm and moving towards those characteristic of very old habitat trees.
6.	Natural beech regeneration is used allowing for a near-natural mixture of indigenous tree species of around 15 %.
7.	To determine, mark and maintain a permanent system of skid trails (with a distance of at least 40 m).
8.	Artificial drainage systems are removed and the natural water regime is restored. Mires and wetlands are maintained within the forest.

Appendix 2 Description of different FDPs according to habitat parameters cited from Begehold et al.. 2016 (following Winter 2005; Winter and Brambach 2011). An FDP patch is recorded with a minimum size of 14 m × 14 m. Canopy cover = canopy cover of all trees with DBH > 7 cm, DBH = diameter at breast height measured at a height of 1.3 m, DBH_{max} = largest DBH within the investigated patch, deadwood = proportion of standing and lying deadwood from the total stock volume within patch. Regeneration includes all tree individuals (except seedlings) and with DBH < 7 cm.

FDP	Parameters
Gap	Canopy cover < 30 %, Regeneration cover < 50 %, any deadwood amount
Regeneration phase	Canopy cover < 30 %, Regeneration cover > 50 %, any deadwood amount
Initial phase	Canopy cover > 30 %, DBH < 20cm, any deadwood amount
Early optimum phase	Canopy cover > 30 %, 20 cm < DBH_{max} ≤ 40 cm, deadwood amount < 30 %
Mid-optimum phase	Canopy cover > 30 %, 40 cm < DBH_{max} ≤ 60 cm, deadwood amount < 30 %
Late optimum phase	Canopy cover > 30 %, DBH_{max} > 60 cm, deadwood amount < 30 %
Terminal phase	Canopy cover > 30 %, DBH_{max} > 60 cm, height > 85% of potential height (= 45 m), deadwood amount < 30 %
Disintegration phase	Canopy cover > 30 %, DBH > 20 cm, deadwood amount > 30 %

Appendix 3 Mean patch sizes ± sd and patch numbers of the single FDPs across all study sites in 2002 and 2012/2013.

FDP	Mean patch size 2002	Patch number 2002	Mean patch size 2012/2013	Patch number 2012/13
Gap	0.046 ± 0.07	223	0.038 ± 0.03	193
Regeneration phase	0.065 ± 0.06	228	0.054 ± 0.06	288
Initial phase	0.414 ± 1.91	96	0.121 ± 0.48	226
Early optimum phase	0.177 ± 0.44	111	0.156 ± 0.56	167
Mid-optimum phase	0.677 ± 3.96	205	0.500 ± 2.89	273
Late optimum phase	0.313 ± 2.62	100	0.139 ± 0.85	424
Terminal phase	0.065 ± 0.10	38	0.078 ± 0.10	56
Disintegration phase	0.037 ± 0.03	97	0.039 ± 0.03	191
Swamps	0.09 ± 0.07	27	0.114 ± 0.13	37
All	0.229 ± 1.92	1,125	0.151 ± 1.16	1,855

Appendix 4 Mean FDP proportions (in per cent) of the single FDPs across management types in 2002 and 2012/2013. Reg = Regeneration phase, Ini = Initial phase, erO = Early optimum phase, mO = Mid-optimum phase, laO = Late optimum phase, Ter = Terminal phase, Dis = Disintegration phase, Sw = Swamps.

Management type	Year	Gap	Reg	Ini	erO	mO	laO	Ter	Dis	Sw
naturalness-promoting	2002	5.6	9.0	14.5	11.6	56.3	1.9	0.0	0.4	0.7
	2012/13	4.2	10.3	7.4	17.6	33.5	25.3	0.0	1.0	0.6
recently unmanaged	2002	3.7	0.2	34.1	5.7	47.4	4.5	1.9	0.6	1.8
	2012/13	1.0	0.7	24.5	6.1	35.9	24.7	1.9	3.0	2.2
long-term unmanaged	2002	3.1	8.2	2.6	8.8	19.9	49.4	2.2	4.8	0.8
	2012/13	2.0	3.3	8.8	5.9	15.3	54.3	3.5	6.2	0.7

SUPPLEMENTARY MATERIAL

Supplementary Material A Study sites, sizes, stand histories (according to Schumacher (2006: 19), H. Schöne: personal communication), and Fagetum associations. [1]Management without nature conservation focus (different management), [2]naturalness-promoting management considering certain management criteria within the last decade (see Table 1), [3]recently unmanaged for 15 years, [4]former shelterwood-logging, [5]recently unmanaged for 22 years (except study site k1: unmanaged for 26 years), [6]long-term unmanaged since 1950 (r1) or at least 1900 (r2 and r3). For further information (altitude, precipitation, nutrition) see Winter (2005: 22).

Study site	Name of the study site	Size [ha]	Forest site for…	Age of the old stock	Origin of the actual old stock	Fagetum association (according to Fischer, 1995)
w1[1]	Lüttenhagen	34.0	more than 200 years	170-180 years	Natural regeneration	Galio odorati
w2[1]	Feldberg	38.8	at least 300 years	170-180 years	Natural regeneration	Galio odorati
w21[1]	Luzin	38.8	at least 300 years	148-178 years	Natural regeneration	Galio odorati
w22[1]	Hinrichshagen	55.5	at least 250 years	119-128 years	Natural regeneration	Luzulo
w3[3]	Thomsdorf	42.0	approx. 200 years	140-160 years	Natural regeneration	Luzulo
w4[3,4]	Haussee	11.4	approx. 200 years	170 years	Natural regeneration	Galio odorati
w6[3,4]	Klasuhagen	17.1	approx. 200 years	180 years	Natural regeneration	Galio odorati
w7[2]	Temmen	40.0	not known; a very long time	160-170 years	Not known	Galio odorati
w8[2]	Suckow	39.4	not known; a very long time	140-160 years	Not known	Galio odorati
w9[2]	Melzow	40.2	all time (since ice age)	140-160 years	Natural regeneration	Galio odorati
w10[2]	Schwarzes Loch	30.4	at least 300 years	145 years	Natural regeneration, planting and seeding	Galio odorati
w11[2]	Senftenthal	45.0	at least 200 years	120-140 years	Natural regeneration and possibly additional planting	Galio odorati
w12[2]	Chorin	40.3	not known; a very long time	180 years	Natural regeneration, planting and seeding	Galio odorati

w13[2]	Eberswalde	34.1	at least 300 years	130-170 years	Natural regeneration	Luzulo
k1[5]	Stechlin	20.1	not known (always?)	150-190 years	Natural regeneration	Luzulo
k2[5]	Grumsin-West	36.5	not known (always?)	150-180 years	Natural regeneration	Galio odorati
k3[5]	Grumsin-Ost	40.3	not known (always?)	140-160 years	Natural regeneration	Galio odorati
k4[5]	Heilige Hallen Erweiterung	13.6	not known (always?)	160-170 years	Natural regeneration	Galio odorati
k5[5]	Fauler Ort Erweiterung	15.2	probably all time (since ice age)	109-135 years	Natural regeneration	Galio odorati
r1[6]	Serrahn	43.1	a long time (always?)	190-200 years	Natural regeneration	Galio odorati
r2[6]	Heilige Hallen (HH)	24.9	approx. 350 years	360 years	Probably natural regeneration	Galio odorati
r3[6]	Fauler Ort (FO)	13.6	all time (since ice age)	310 years	Probably natural regeneration	Galio odorati

Supplementary Material B Breeding bird abundances (i.e. number of territories per 10 ha) in 20 lowland beech forest sites. Bird survey was performed 2012 or 2013. Species abbreviations are given as the EURING (European Union for Bird Ringing) code: AEGCAU *Aegithalos caudatus*, ANACRE *Anas crecca*, ANAPLA *Anas platyrhynchos*, ANTTRI *Anthus trivialis*, BUCCLA *Bucephala clangula*, BUTBUT *Buteo buteo*, CERBRA *Certhia brachydactyla,* CERFAM *Certhia familiaris,* COCCOC *Coccothraustes coccothraustes,* COLOEN *Columba oenas,* COLPAL *Columba palumbus,* CORCOR *Corvus corax,* CUCCAN *Cuculus canorus,* DENMAJ *Dendrocopos major,* DENMED *Dendrocopos medius,* DENMIN *Dendrocopos minor*, DRYMAR *Dryocopus martius,* ERIRUB *Erithacus rubecula,* FALSUB *Falco subbuteo,* FICHYP *Ficedula hypoleuca,* FICPAR *Ficedula parva,* FRICOE *Fringilla coelebs,* GARGLA*, Garrulus glandarius,* GRUGRU *Grus grus,* MILMIL *Milvus milvus,* MUSSTR *Muscicapa striata,* ORIORI *Oriolus oriolus,* PARCAE *Parus caeruleus,* PARMAJ *Parus major,* PERATE *Periparus ater,* PHOPHO *Phoenicurus phoenicurus,* PHYCOL *Phylloscopus collybita,* PHYSIB *Phylloscopus sibilatrix,* PHYTRO *Phylloscopus trochilus,* PICVIR *Picus viridis*, POEPAL *Poecile palustris,* PYRPYR *Pyrrhula pyrrhula*, REGIGN *Regulus ignicapilla,* REGREG *Regulus regulus,* SITEUR *Sitta europaea,* STRALU *Strix aluco,* STUVUL *Sturnus vulgaris, SYLBOR Sylvia borin,* SYLATR *Sylvia atricapilla,* TACRUF *Tachybaptus ruficollis,* TRIOCH *Tringa ochropus,* TROTRO *Troglodytes troglodytes,* TURMER *Turdus merula,* TURPHI *Turdus philomelos,* TURVIS *Turdus viscivorus.*

Study site	Breeding bird abundances [number of territories per 10 ha]																							
	ANA PLA	ANA CRE	BUC CLA	TAC RUF	MIL MIL	BUT BUT	FAL SUB	GRU GRU	TRI OCH	COL OEN	COL PAL	CUC CAN	STR ALU	DRY MAR	PIC VIR	DEN MAJ	DEN MED	DEN MIN	ANT TRI	ERI RUB	PHO PHO	TUR PHI	TUR VIS	TUR MER	SYL BOR
w4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	5.3	0.0	0.9	0.0	2.6	0.0
w6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	1.2	0.0	0.0	0.6	0.0	1.2	0.0	0.0	0.0	5.3	0.0	1.8	0.0	1.8	0.0
w1	0.3	0.0	0.3	0.0	0.0	0.6	0.0	0.3	0.0	0.6	0.9	0.0	0.3	0.6	0.0	2.1	0.0	0.3	0.0	3.8	0.0	2.4	0.0	2.4	0.0
w2	0.3	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.3	1.0	0.0	0.3	0.5	0.0	2.8	0.0	0.0	0.0	4.6	0.3	1.0	0.0	2.1	0.0
w7	0.0	0.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0	2.0	1.8	0.0	0.5	0.5	0.5	2.5	0.8	0.5	0.5	7.8	0.0	1.8	0.0	2.8	0.0
w8	0.3	0.0	0.3	0.0	0.0	0.3	0.0	0.3	0.0	1.0	0.8	0.0	0.3	0.8	0.5	3.0	1.3	0.3	0.0	7.8	0.0	2.3	0.0	3.0	1.3
w9	0.0	0.0	0.2	0.0	0.0	0.5	0.0	0.0	0.0	1.0	0.7	0.0	0.0	0.7	0.2	2.7	0.5	0.0	0.0	6.2	0.0	3.2	0.0	4.0	1.0
w10	0.0	0.0	0.3	0.0	0.0	0.3	0.0	0.0	0.0	1.3	1.0	0.3	0.3	0.3	0.0	2.6	0.3	0.0	0.0	8.6	0.0	2.0	0.0	3.0	0.0
w11	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.4	0.0	0.2	0.2	0.2	2.2	0.4	0.0	0.0	7.1	0.0	1.3	0.0	1.3	0.0
w12	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.2	0.0	1.0	0.7	0.0	0.2	0.2	0.0	3.2	0.5	0.0	0.0	6.2	0.0	1.0	0.0	2.2	0.0
w13	0.3	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.6	1.7	0.0	0.3	0.3	0.0	2.3	0.0	0.0	0.0	5.8	0.0	0.9	0.0	2.9	0.0
k1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.5	0.0	0.5	0.5	0.0	2.0	0.5	0.5	0.0	5.5	0.0	2.0	0.0	3.0	0.0
k2	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.0	0.0	1.0	0.5	0.0	0.2	0.0	0.0	2.0	0.5	0.0	0.0	3.5	0.0	0.7	0.0	0.7	0.0
k3	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.2	1.0	0.5	0.0	0.5	0.5	0.0	1.7	0.2	0.0	0.0	3.7	0.0	0.7	0.0	1.5	0.0
k4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.7	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	8.0	0.0	1.5	0.0	1.5	0.0
w3	0.2	0.0	0.2	0.0	0.0	0.2	0.2	0.5	0.0	1.2	0.5	0.0	0.2	0.2	0.2	2.6	1.0	0.0	0.0	4.3	0.0	1.4	0.0	2.1	0.0
r1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	0.6	0.0	0.3	0.6	0.3	3.7	0.9	0.3	0.0	6.1	0.0	2.4	0.6	5.5	0.0
r2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	2.4	0.0	0.8	0.4	0.0	2.8	1.6	0.4	0.0	8.0	0.0	2.4	0.0	3.6	0.0
r3	0.0	0.0	0.7	0.0	0.7	0.0	0.0	0.0	0.0	6.6	5.1	0.0	0.7	0.7	0.7	2.9	2.9	0.0	0.0	11.8	0.0	2.2	0.0	4.4	0.0

Supplementary Material B (Continuation)

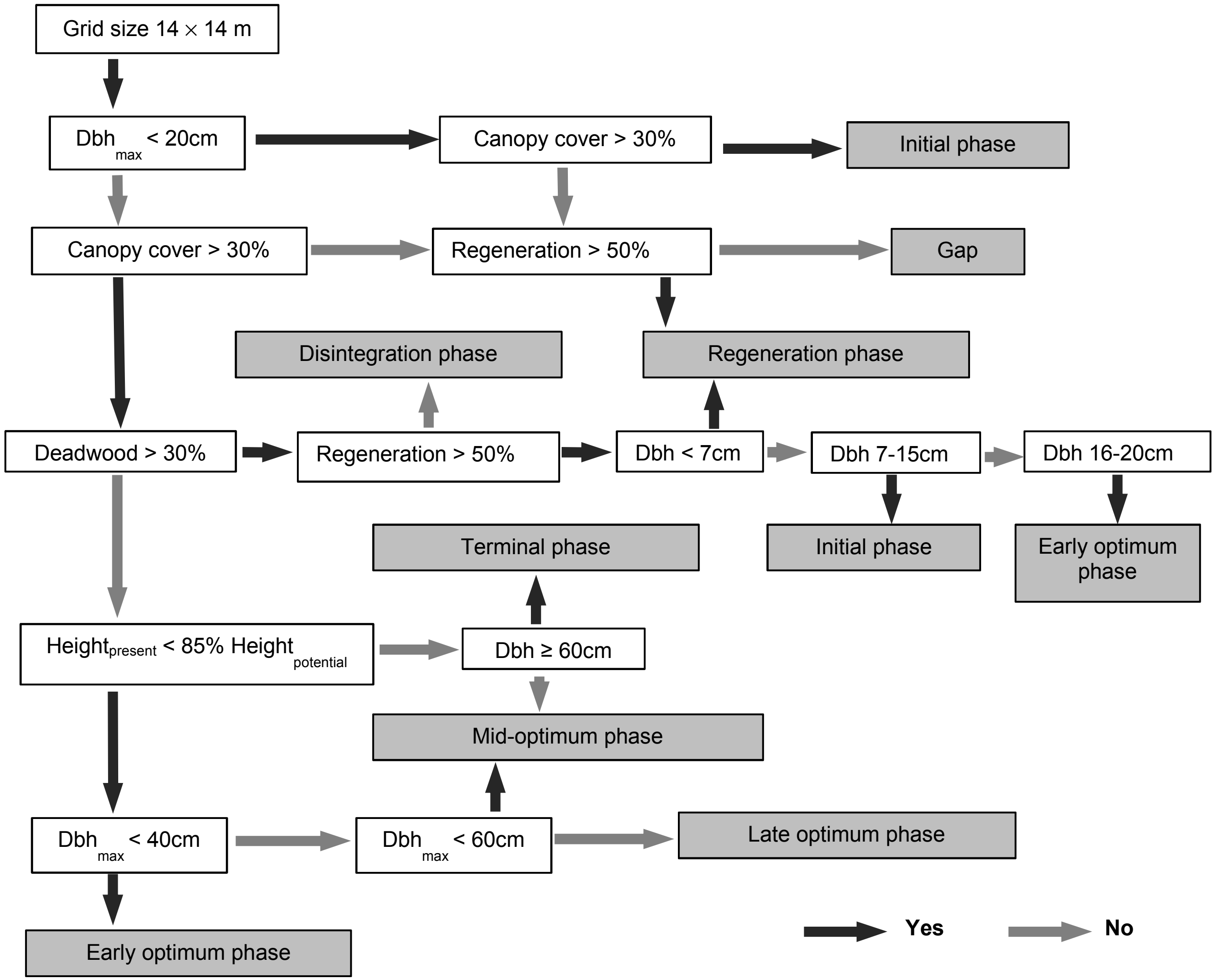
Study site	Breeding bird abundances [number of territories per 10 ha]																								
	SYL ATR	PHY TRO	PHY SIB	PHY COL	REG REG	REG IGN	TRO TRO	MUS STR	FIC PAR	FIC HYP	PAR MAJ	PER ATE	PAR CAE	POE PAL	AEG CAU	SIT EUR	CER FAM	CER BRA	GAR GLA	COR COR	STU VUL	ORI ORI	FRI COE	PYR PYR	COC COC
w4	3.5	0.0	0.0	2.6	0.0	0.0	0.9	0.9	0.0	0.0	3.5	0.0	1.8	0.9	0.9	0.9	0.0	0.0	0.9	0.0	0.0	0.0	4.4	0.0	0.0
w6	5.9	0.0	0.0	2.4	0.0	0.0	0.6	0.6	0.0	0.0	5.9	0.0	4.1	1.8	0.6	2.4	1.2	0.0	1.2	0.0	0.0	0.0	5.3	0.0	1.8
w1	4.1	0.0	0.0	3.2	0.0	0.3	1.8	0.6	0.0	0.0	9.1	0.0	4.7	1.8	0.3	2.1	1.5	0.0	0.6	0.3	0.0	0.0	7.4	0.0	1.2
w2	4.1	0.0	0.0	1.8	0.3	1.0	2.6	0.3	0.0	0.0	7.2	0.3	1.5	0.8	0.0	3.4	1.5	0.5	0.5	0.0	0.5	0.0	7.2	0.0	1.0
w7	10.0	0.0	1.8	5.0	0.0	0.5	1.8	1.3	0.0	0.3	5.8	0.0	5.0	1.5	0.3	4.3	2.3	0.8	0.5	0.3	4.5	0.3	10.8	0.0	1.0
w8	9.4	0.0	0.0	4.6	0.0	1.0	2.3	1.8	0.3	0.0	6.3	0.0	5.6	1.0	0.0	4.8	3.3	1.0	0.5	0.3	2.5	0.3	10.4	0.0	1.8
w9	12.7	0.0	0.0	5.7	0.0	0.5	0.0	1.2	0.0	0.0	11.9	0.0	8.5	1.5	0.2	4.0	2.5	0.0	0.7	0.2	0.0	0.2	7.5	0.0	1.7
w10	7.9	0.0	8.2	1.0	0.0	0.7	5.9	3.3	0.7	0.3	10.2	0.0	5.9	1.3	0.3	3.0	5.9	1.3	0.7	0.3	2.3	0.3	14.8	0.0	2.3
w11	8.4	0.0	2.0	1.8	0.0	1.6	1.3	1.6	0.0	0.0	6.9	1.1	3.6	0.9	0.0	2.2	2.4	0.9	0.2	0.0	1.6	0.9	13.1	0.0	1.6
w12	5.0	0.0	0.0	0.7	0.0	0.2	1.7	2.7	0.0	0.2	10.2	0.0	5.7	0.7	0.0	3.5	2.0	0.0	0.5	0.0	0.0	0.5	8.9	0.0	1.5
w13	5.2	0.9	2.3	1.5	0.0	0.9	1.7	1.2	0.0	0.0	7.3	0.0	3.8	1.7	0.3	3.8	2.3	0.0	0.3	0.0	0.3	0.3	12.2	0.3	1.2
k1	3.5	0.0	1.0	0.0	0.0	0.0	3.0	2.0	0.0	1.5	7.5	1.0	6.0	1.5	0.0	3.0	2.0	1.0	0.5	0.0	0.0	0.0	20.4	0.0	2.5
k2	1.0	0.0	1.0	0.7	0.0	0.7	2.5	1.7	1.0	0.2	6.2	0.0	3.2	0.7	0.0	3.5	2.5	0.0	0.2	0.2	0.0	0.2	10.7	0.0	2.2
k3	2.7	0.0	3.0	0.2	0.0	0.7	2.5	1.5	0.0	0.2	5.5	0.5	3.7	1.2	0.2	2.5	2.0	1.5	0.2	0.0	0.2	0.2	13.7	0.0	2.0
k4	7.3	0.0	7.3	3.6	0.7	2.2	3.6	1.5	0.0	0.0	6.6	1.5	2.2	1.5	0.0	3.6	3.6	0.0	0.7	0.0	0.0	0.0	10.2	0.0	1.5
w3	1.9	0.0	0.7	0.5	0.0	0.2	1.4	1.0	0.2	0.0	5.0	0.0	3.8	1.7	0.0	4.3	3.3	1.9	0.7	0.0	0.0	0.2	9.5	0.0	1.2
r1	1.8	0.0	1.8	0.0	0.0	0.9	4.3	0.3	0.3	0.3	7.0	0.3	6.4	1.2	0.0	4.9	3.0	2.4	1.2	0.0	0.0	0.0	17.1	0.0	3.4
r2	6.0	0.0	6.8	0.8	0.0	0.4	4.0	0.8	0.0	0.0	8.0	0.4	4.0	0.8	0.0	4.8	4.8	0.4	1.2	0.4	3.2	0.4	8.8	0.0	0.8
r3	13.2	0.0	0.7	4.4	0.0	0.0	9.6	3.7	0.0	0.7	10.3	0.0	12.5	2.9	0.7	8.1	8.8	4.4	0.7	0.0	11.8	0.7	16.9	0.0	2.9

Supplementary Material C Sum of *d* values (significant differences, determined as decreasing (-1), constant (0) or increasing (1) of breeding bird abundances in comparison to the trend according to TRIM) for the most common 34 breeding bird species with a presence in at least nine study sites during the first (1998-2002) and/or the second record (2012/13). Breeding guilds are free breeders (F), hole breeders (H), ground breeders (G) and niche breeders (N). Beech forest indicator species (Flade 1994) are shown in bold.

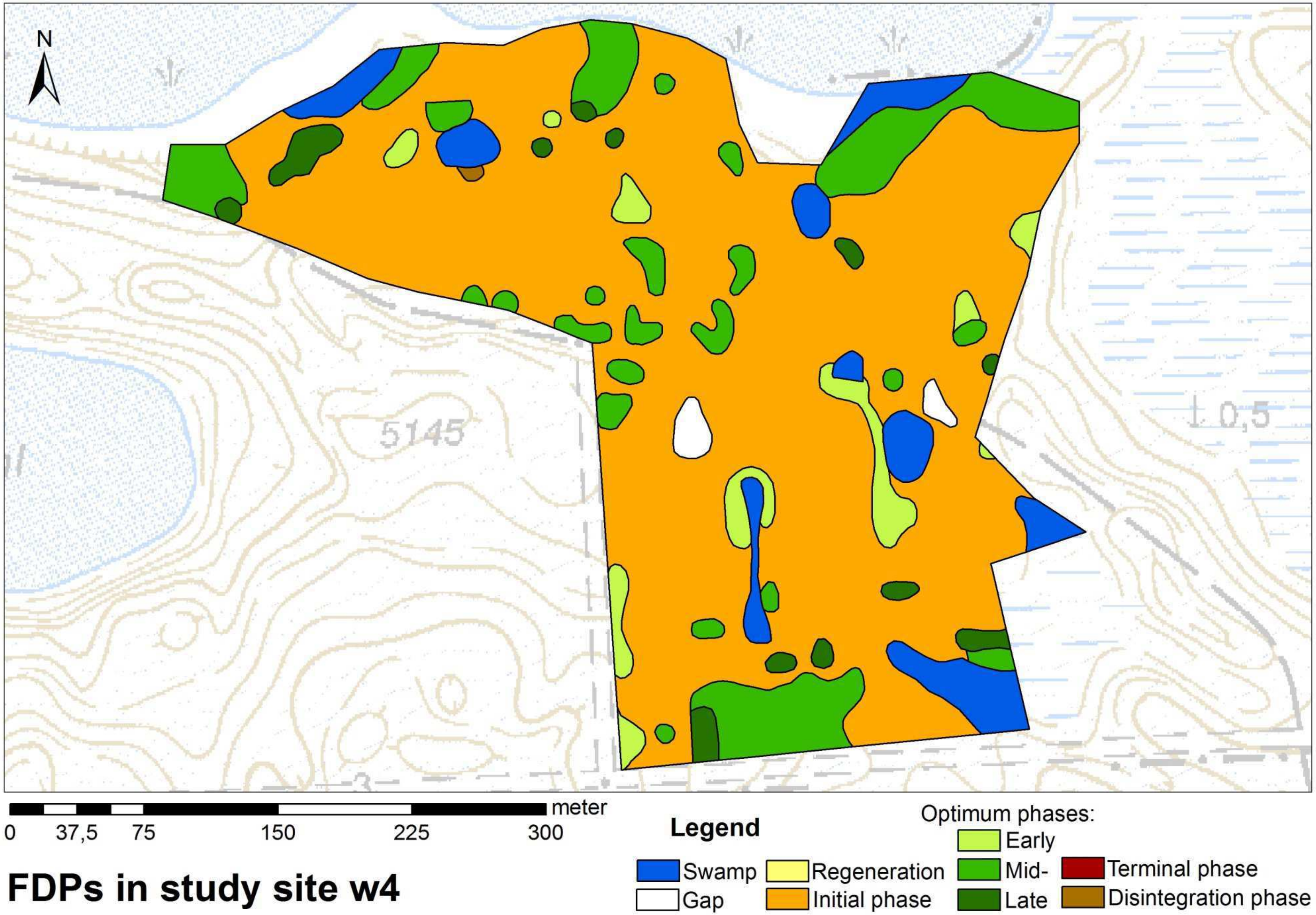
Species (present in at least 9 study sites); common species names	Management types					Breeding guild
	differently managed (n=2)	naturalness-promoting management (n=7)	former shelterwood logging (n=2)	recently unmanaged (n=4)	long-term unmanaged (n=3)	
Common Goldeneye	0	1	0	0	-1	H
Common Buzzard	1	1	0	0	-1	F
Stock Dove	**0**	**4**	**1**	**1**	**2**	**H**
Common Wood Pigeon	1	2	-1	1	0	F
Black Woodpecker	**2**	**2**	**0**	**0**	**0**	**H**
European Green Woodpecker	0	0	-2	-1	0	H
Great Spotted Woodpecker	**2**	**5**	**1**	**0**	**1**	**H**
Middle Spotted Woodpecker	**0**	**0**	**0**	**0**	**0**	**H**
Lesser Spotted Woodpecker	**0**	**-1**	**0**	**0**	**-1**	**H**
European Robin	0	7	1	3	1	G
Song Thrush	2	7	2	1	1	F
Common Blackbird	-1	5	0	3	2	F
Eurasian Blackcap	0	7	-2	2	0	F
Wood Warbler	**-1**	**4**	**0**	**1**	**1**	**G**
Common Chiffchaff	2	5	-2	1	0	G
Common Firecrest	0	3	0	1	0	F
Eurasian Wren	-1	0	0	1	0	N
Spotted Flycatcher	**0**	**5**	**2**	**3**	**1**	**N**
Red-breasted Flycatcher	**0**	**1**	**0**	**0**	**0**	**N**
European Pied Flycatcher	0	2	0	0	1	H

Great Tit	2	5	2	3	2	H
Coal Tit	-1	-1	0	0	-1	H
Eurasian Blue Tit	1	5	2	4	2	H
Marsh Tit	**1**	**3**	**-1**	**1**	**0**	**H**
Long-tailed Tit	0	3	0	1	1	F
Eurasian Nuthatch	**1**	**3**	**0**	**4**	**1**	**H**
Eurasian Treecreeper	1	7	0	3	2	N
Short-toed Treecreeper	**0**	**1**	**-1**	**2**	**2**	**N**
Eurasian Jay	0	3	1	2	2	F
Common Starling	0	-2	-2	-1	-1	H
Eurasian Golden Oriole	0	1	0	1	1	F
Common Chaffinch	2	7	1	4	2	F
Hawfinch	2	6	1	3	2	F

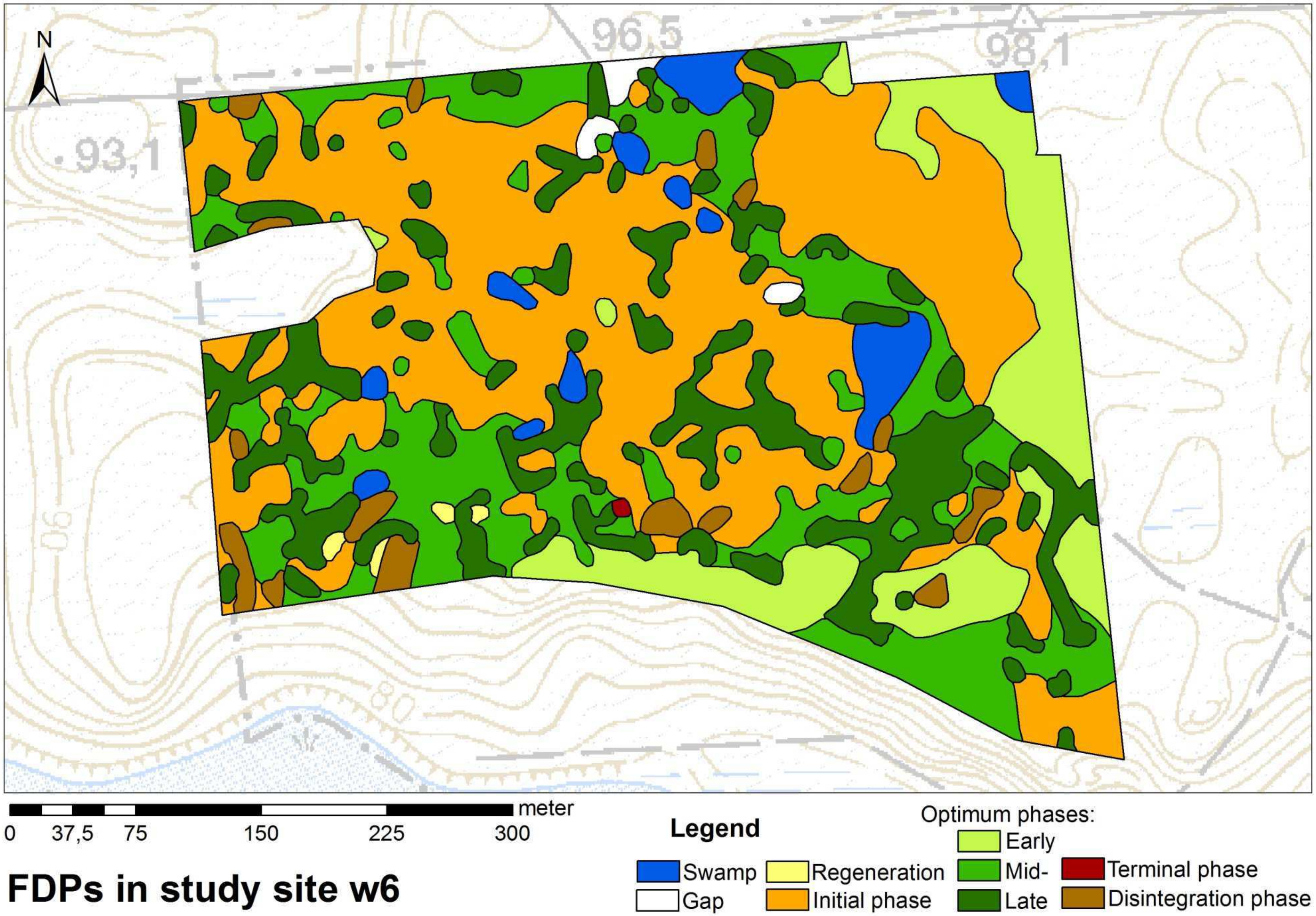
Supplementary Material D Flowchart to map FDPs. Canopy cover of all trees with dbh > 7 cm on patch; dbh = diameter at breast height measured in 1.3 m; Dbh_{max} = largest dbh on the patch; Deadwood = Proportion of standing and lying deadwood on the total stock volume. Regeneration includes all tree individuals after the seedlings stage and with dbh < 7 cm. Figure modified according to Winter (2005: 28).



Supplementary Material E Maps of FDPs in 22 lowland beech forest sites.



Supplementary Material E Maps of FDPs in 22 lowland beech forest sites.



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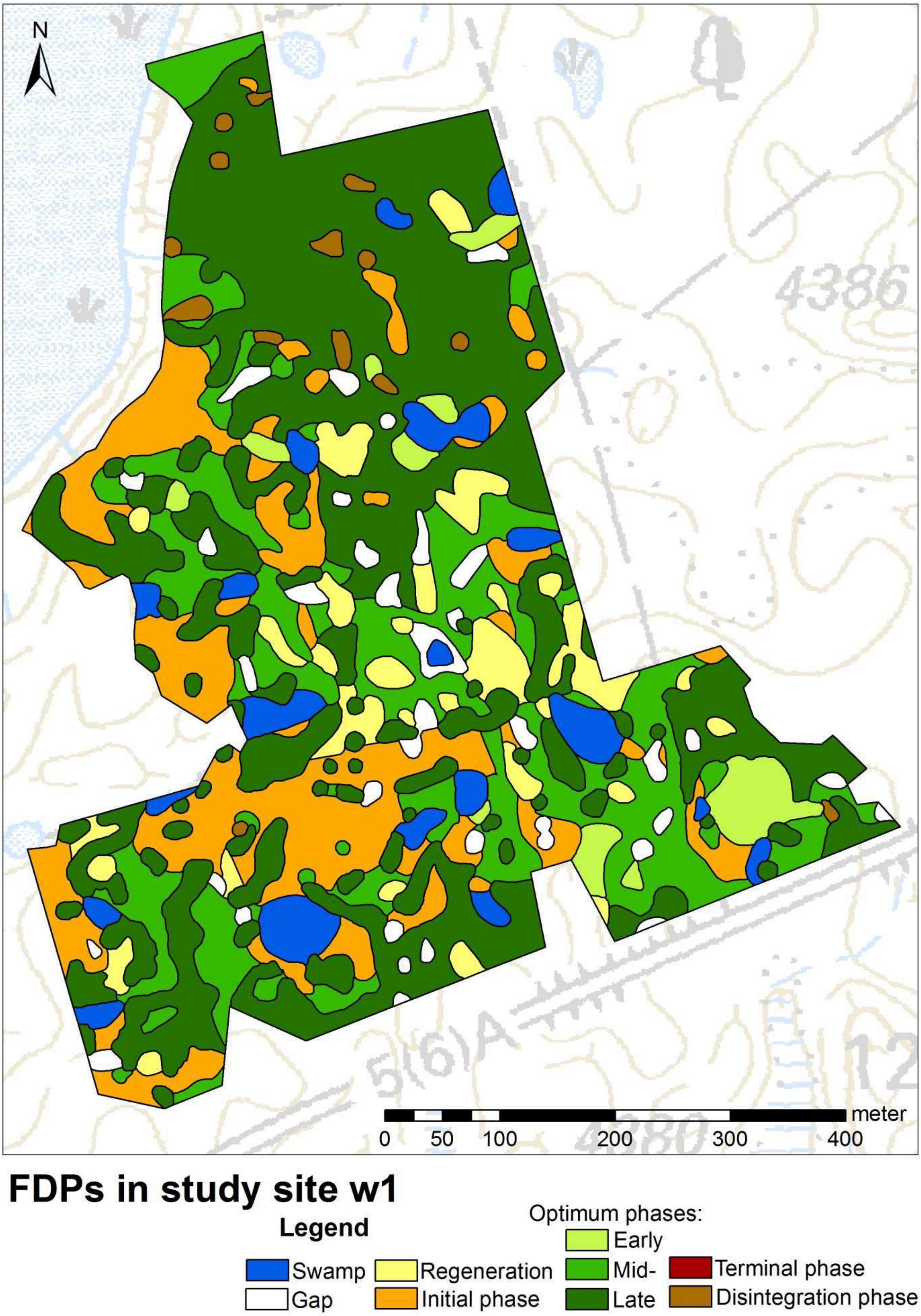

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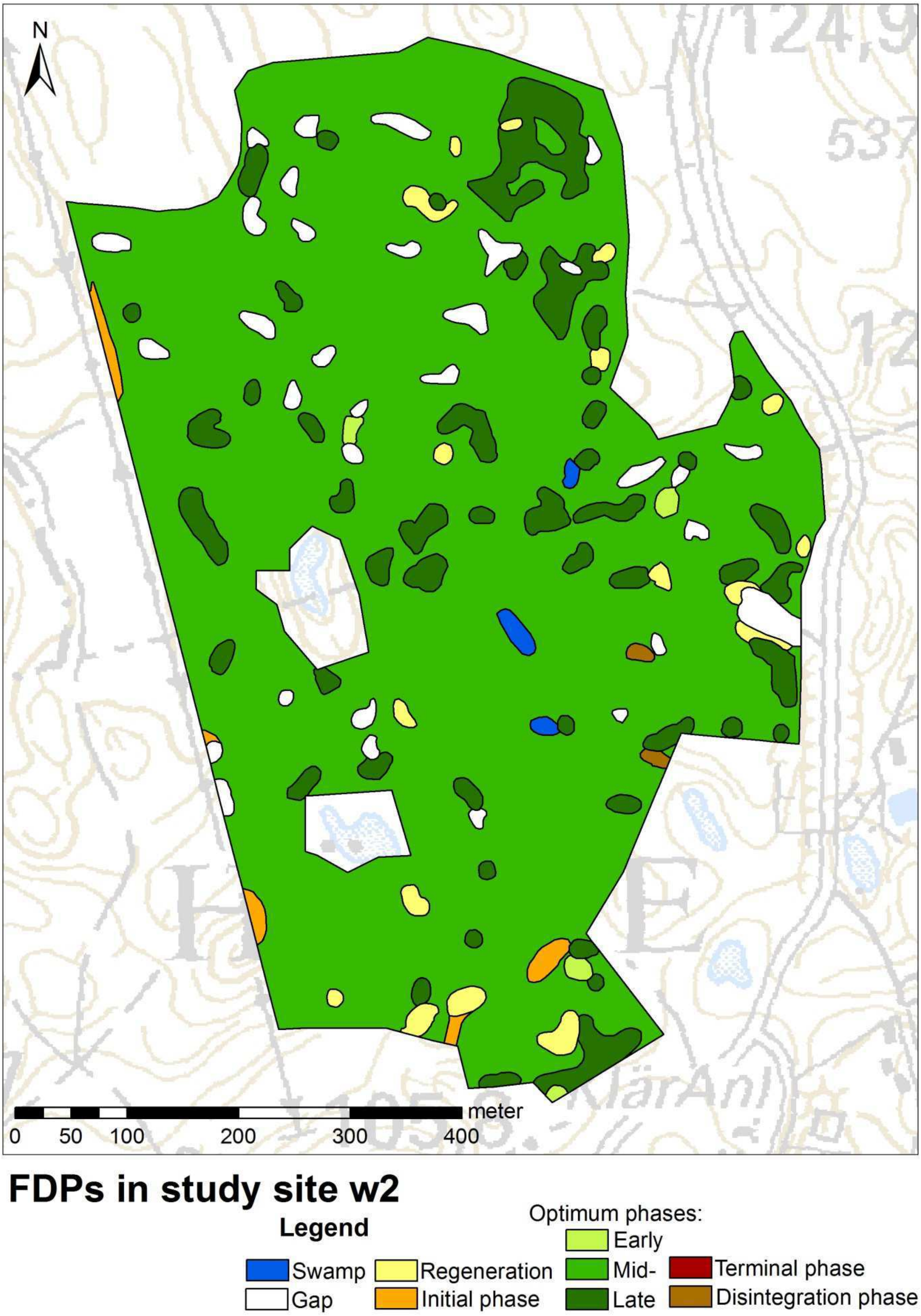

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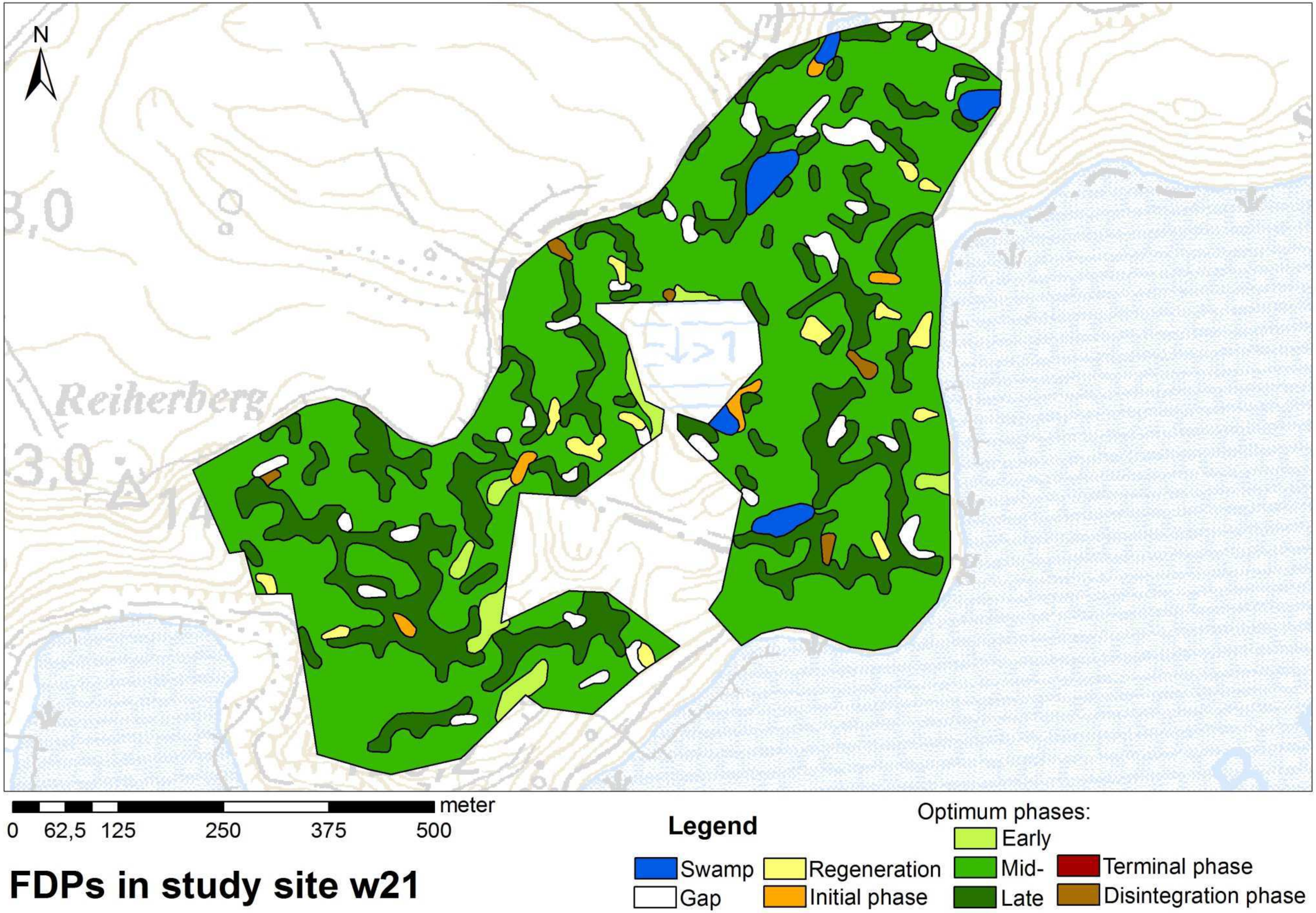

FDPs in study site w21

Supplementary Material E Maps of FDPs in 22 lowland beech forest sites.

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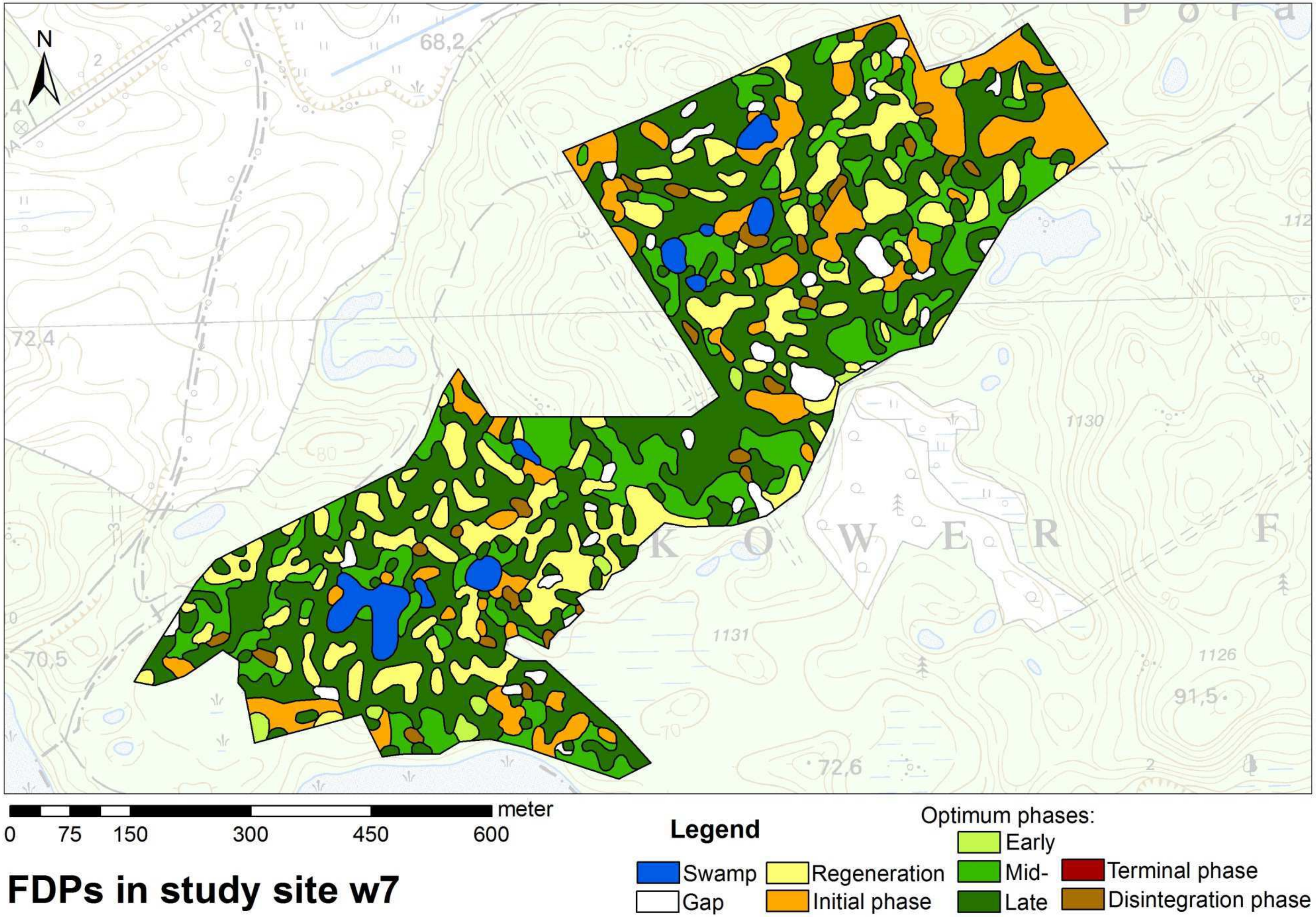

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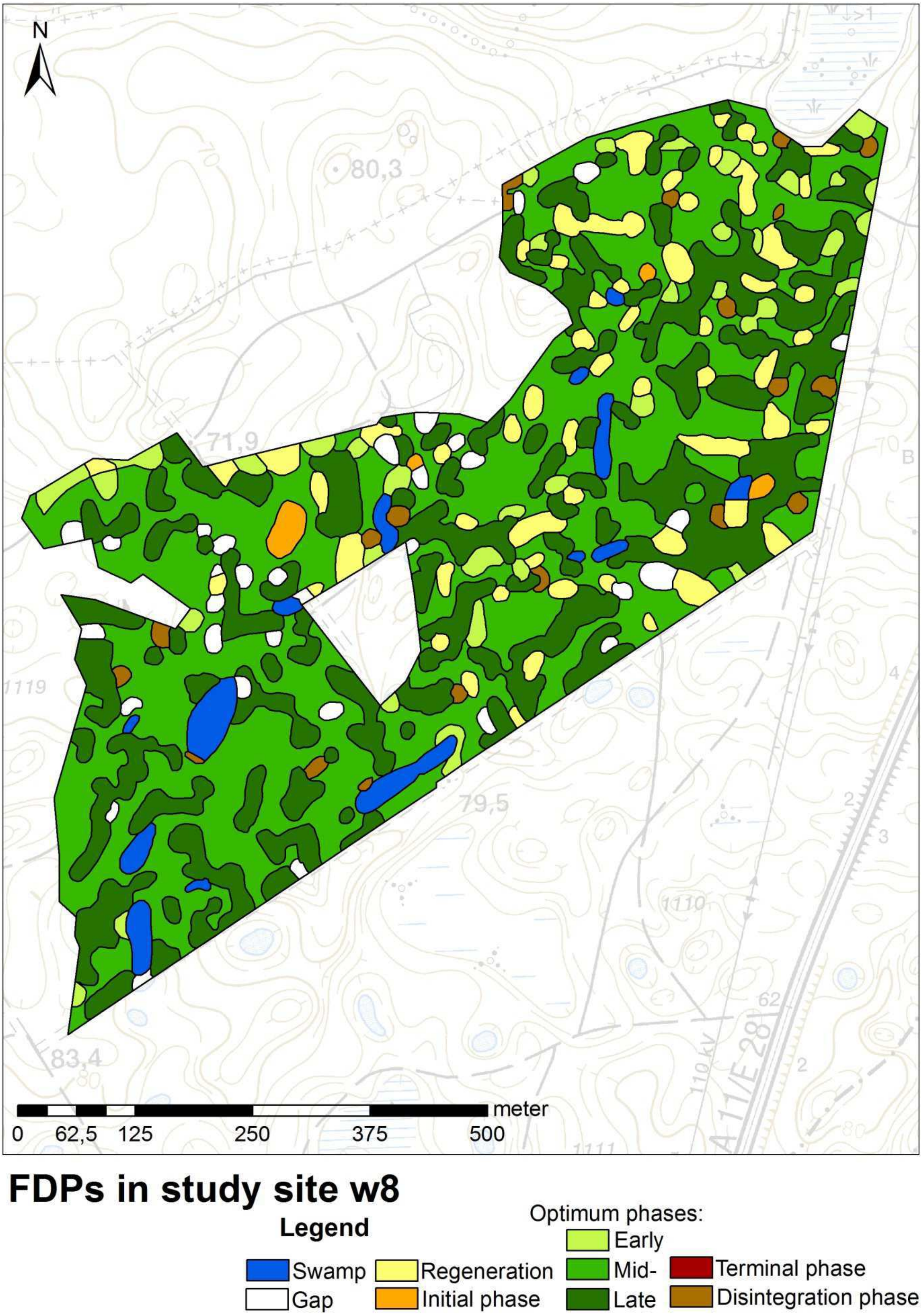

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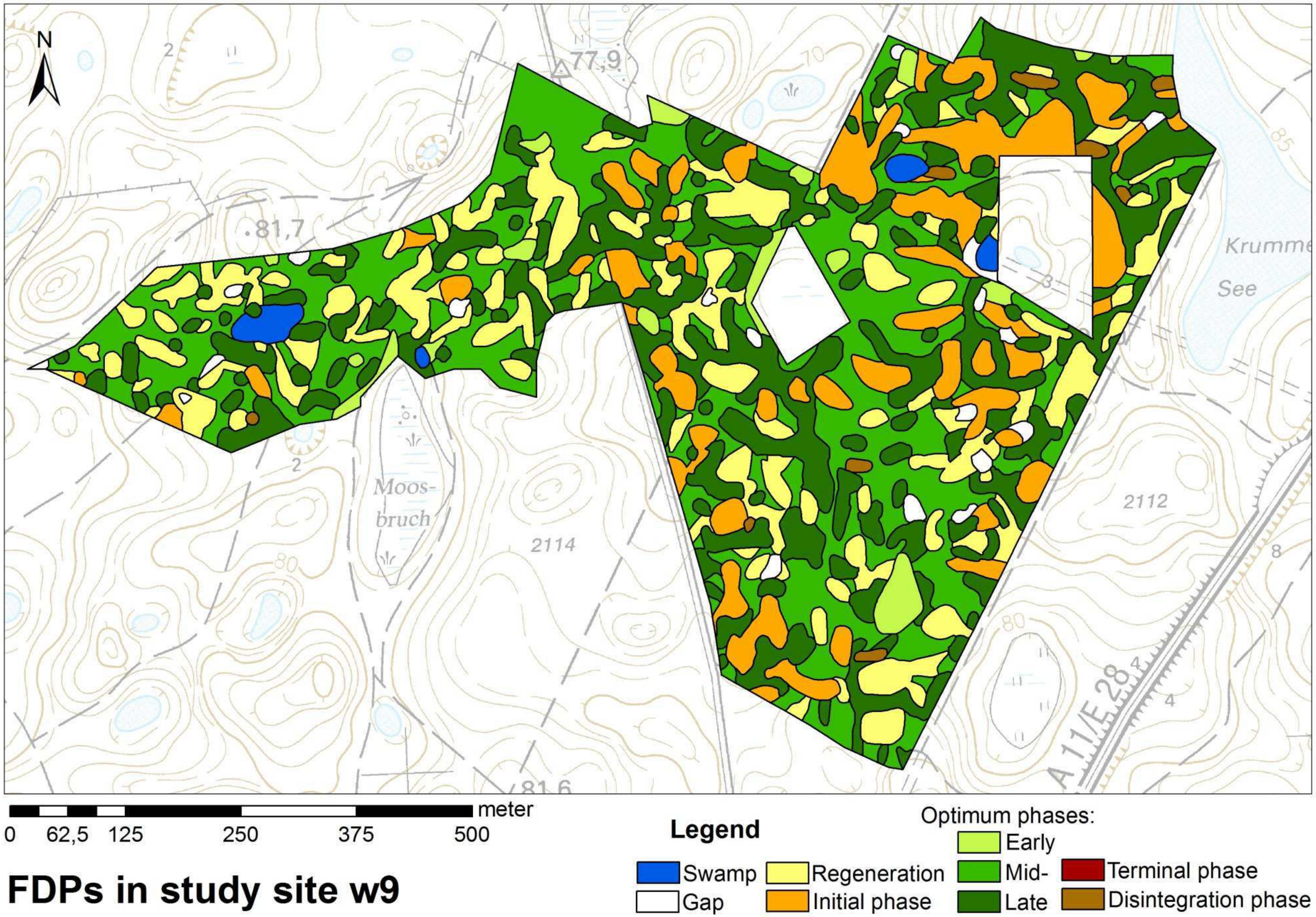

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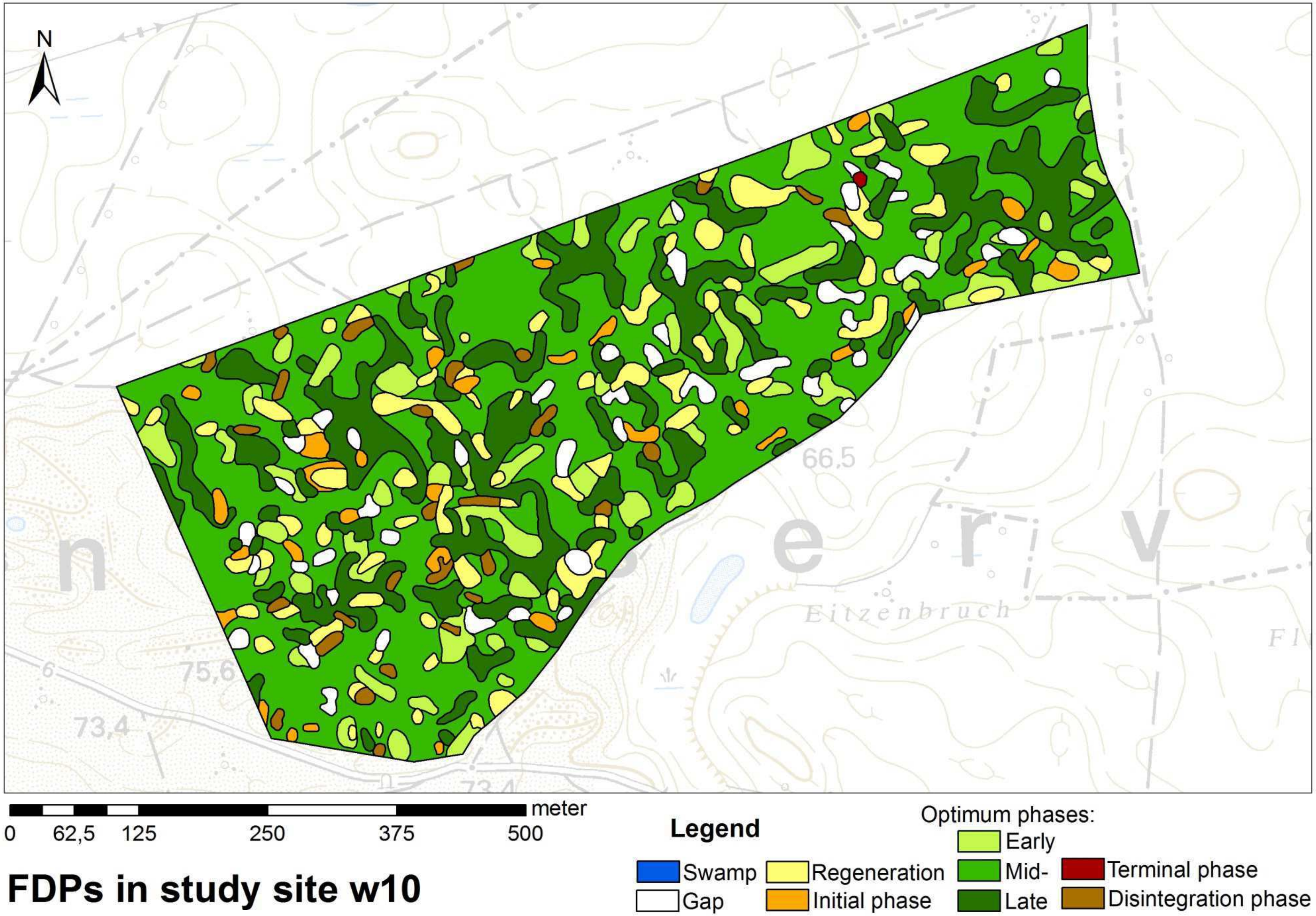

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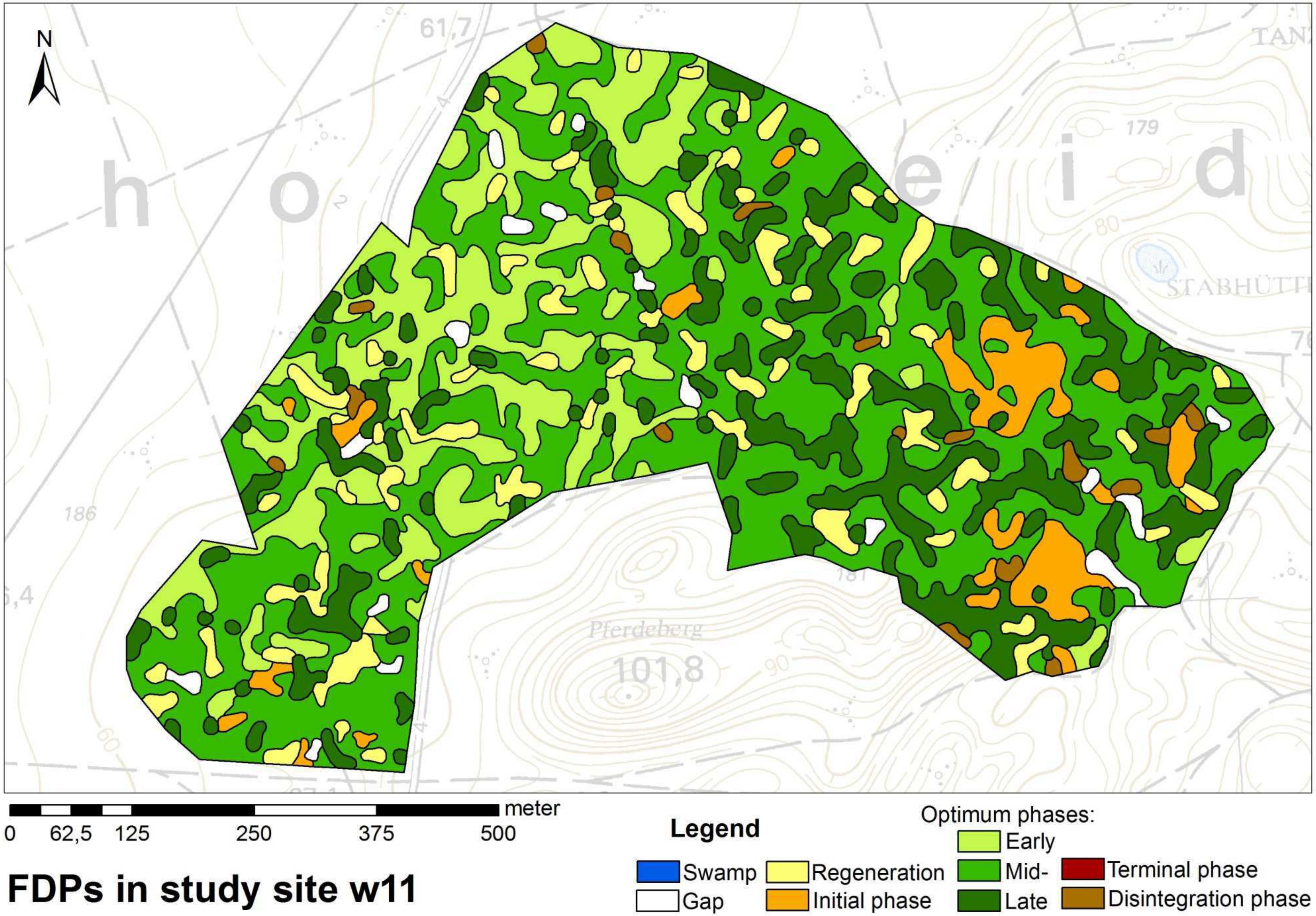

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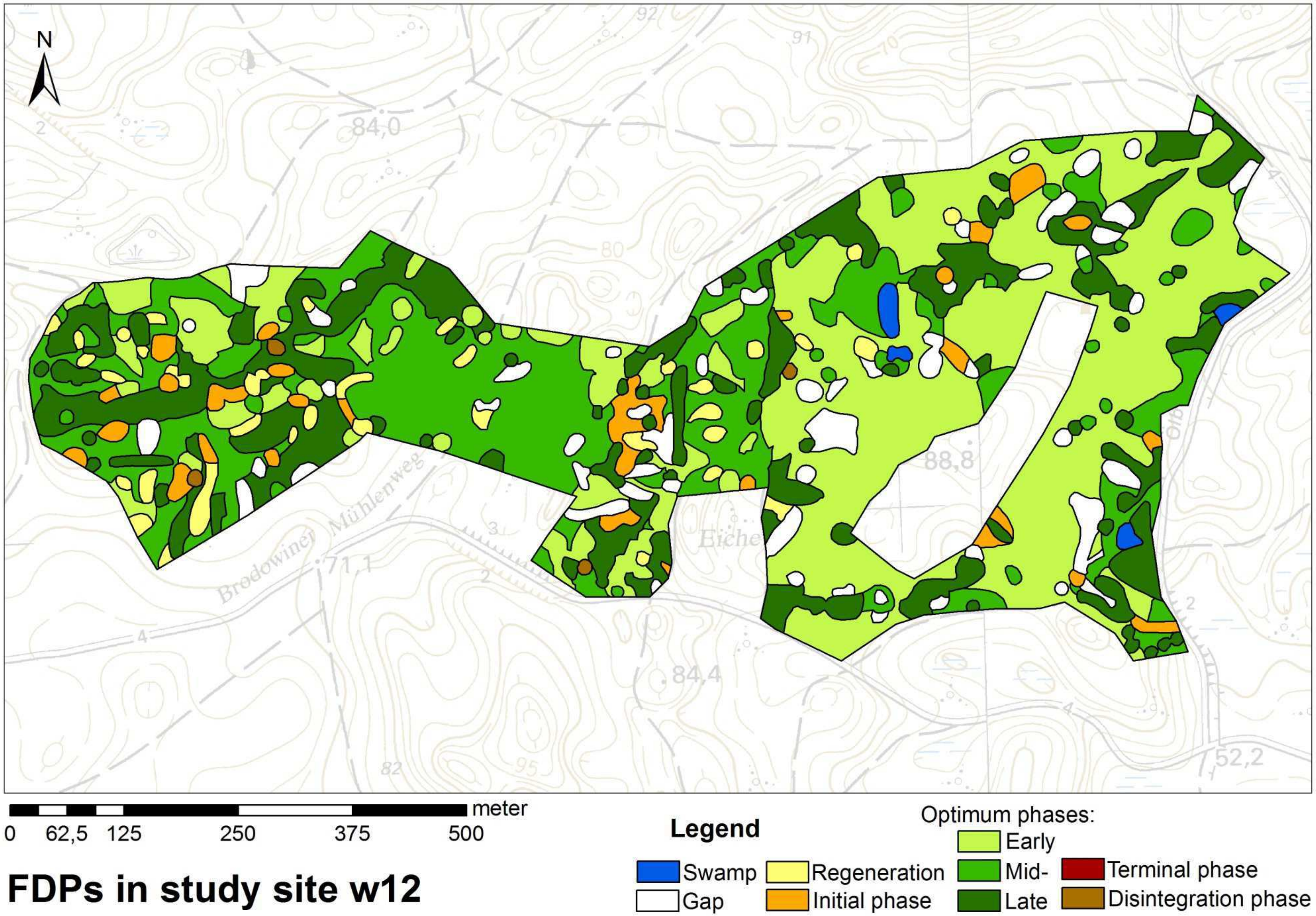

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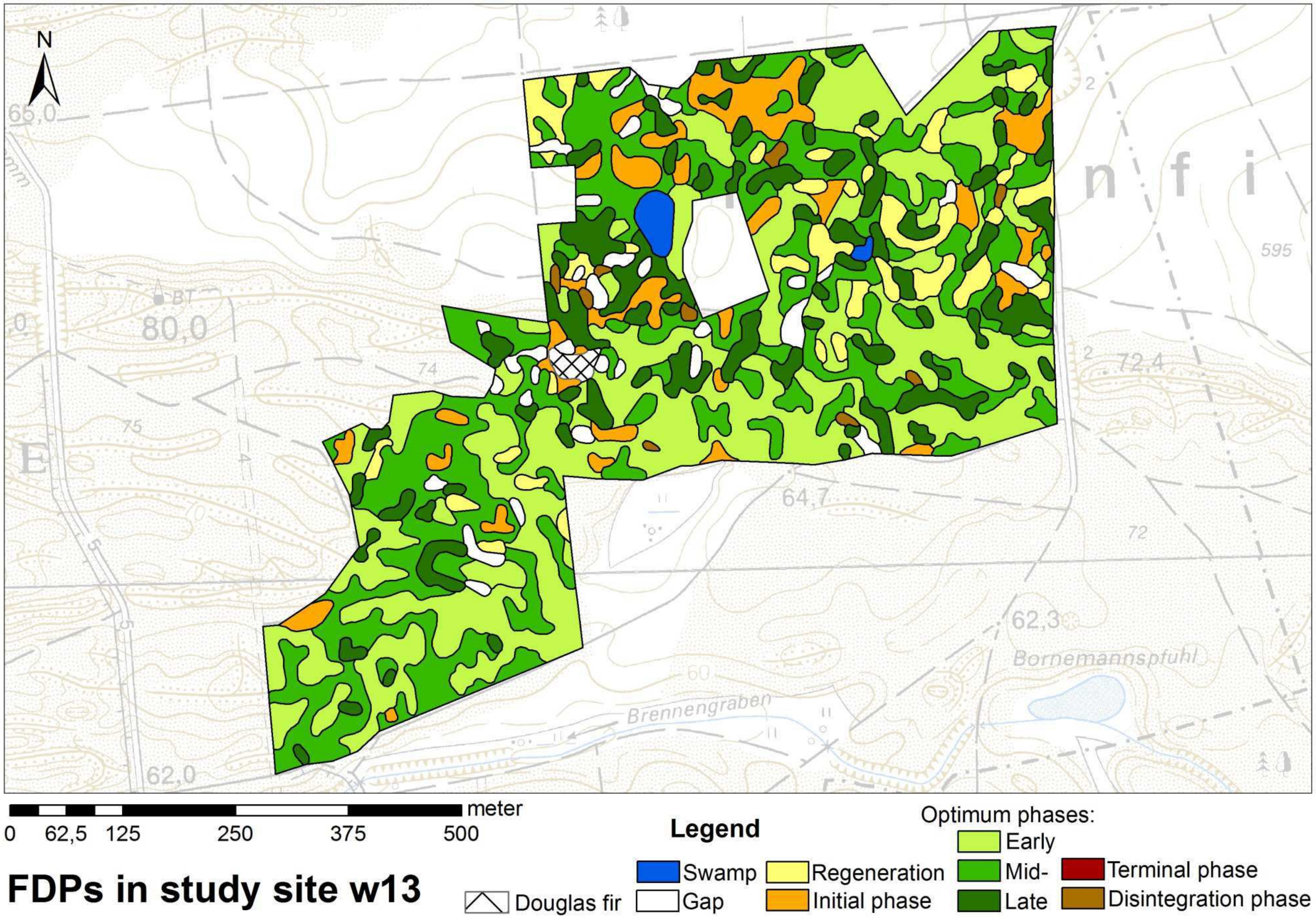

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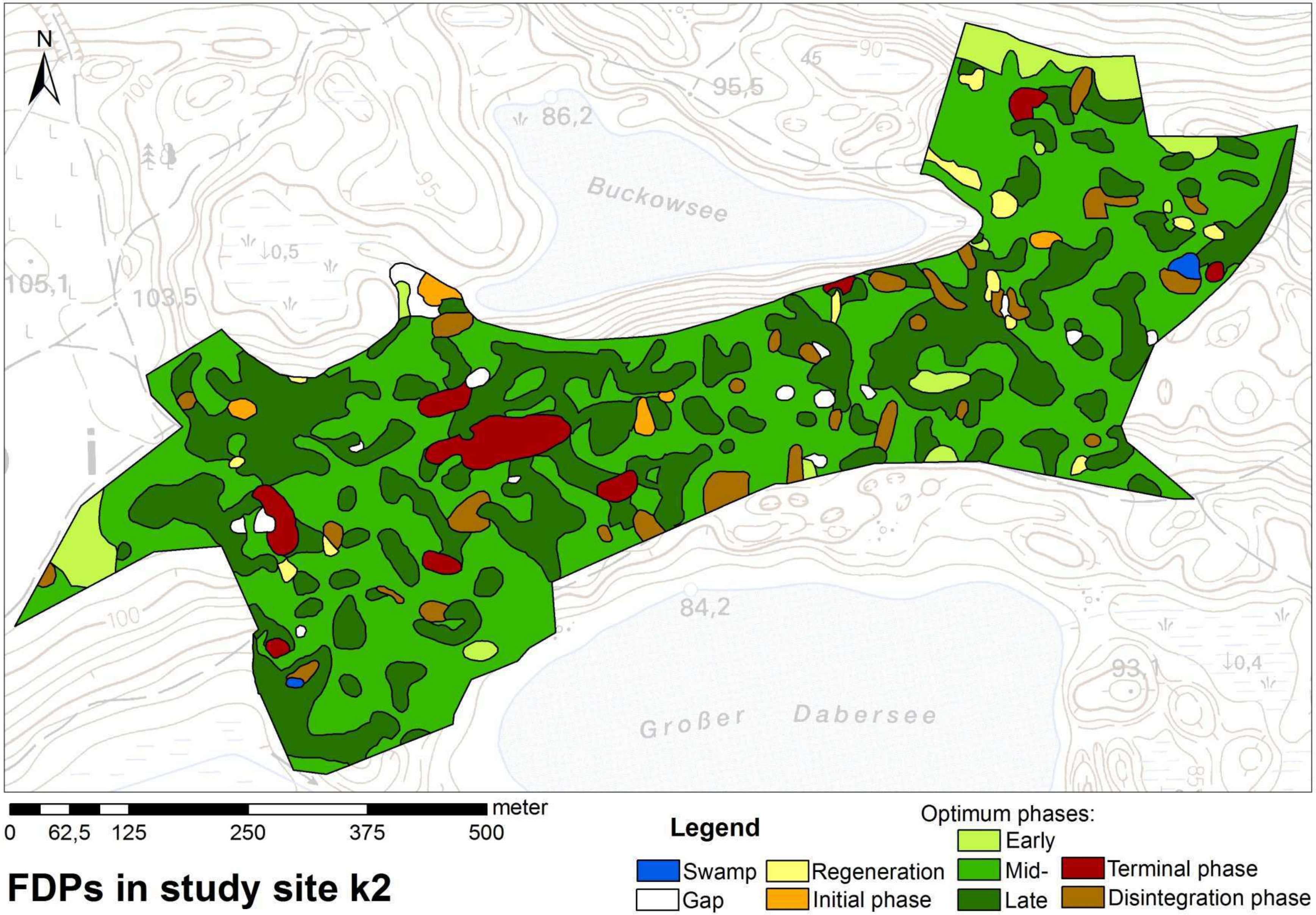

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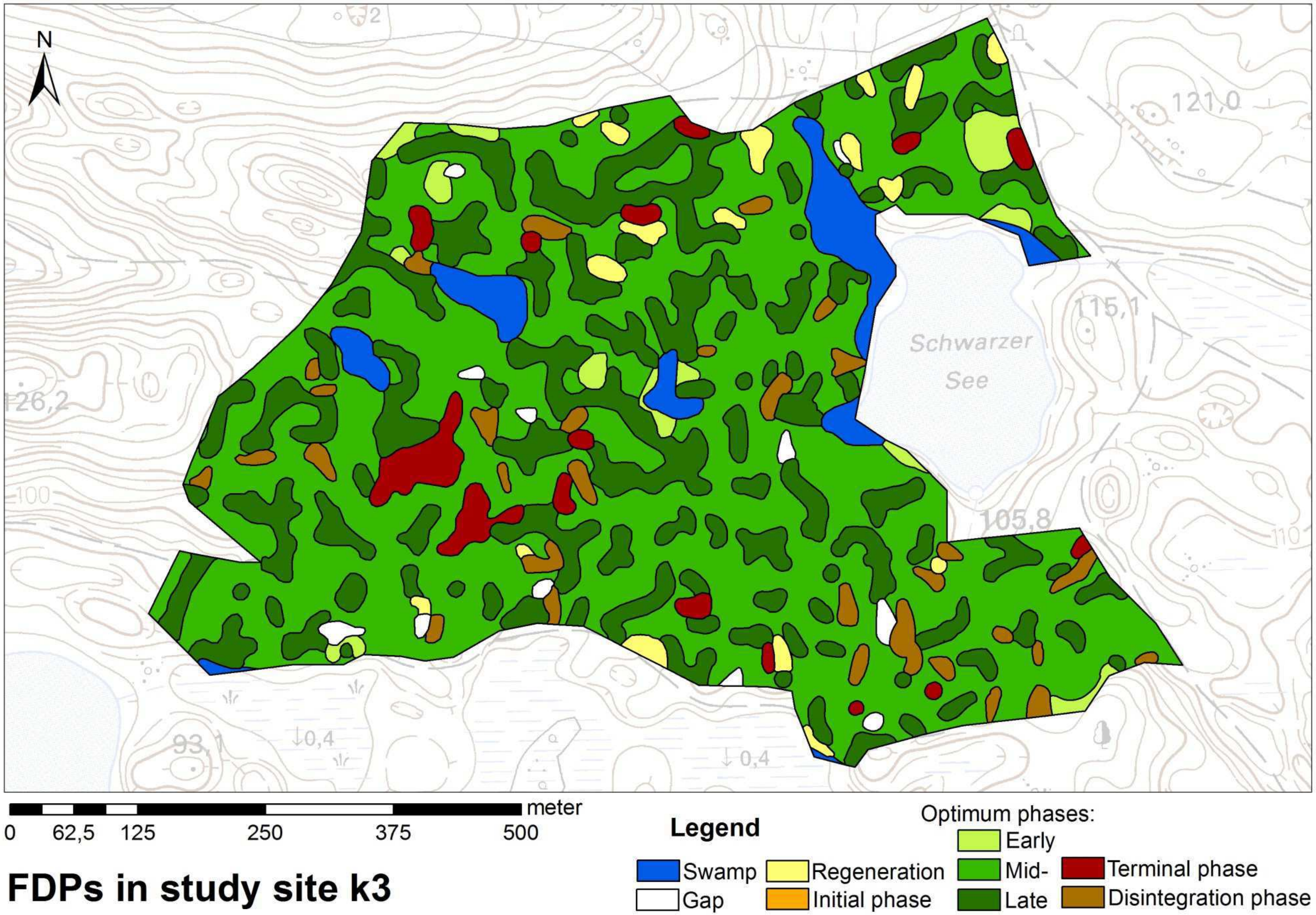

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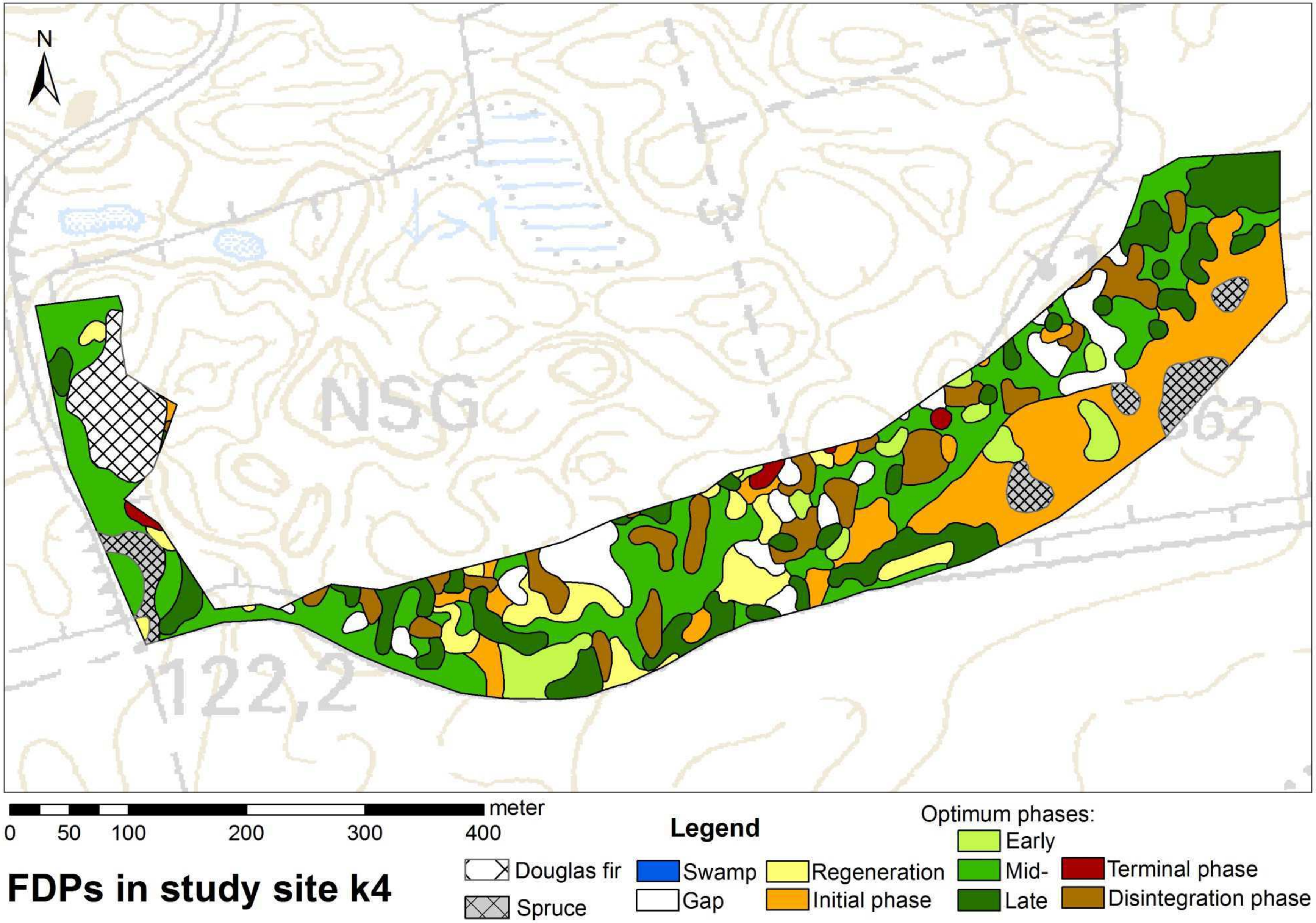

Supplementary Material E Maps of FDPs in 22 lowland beech forest sites.

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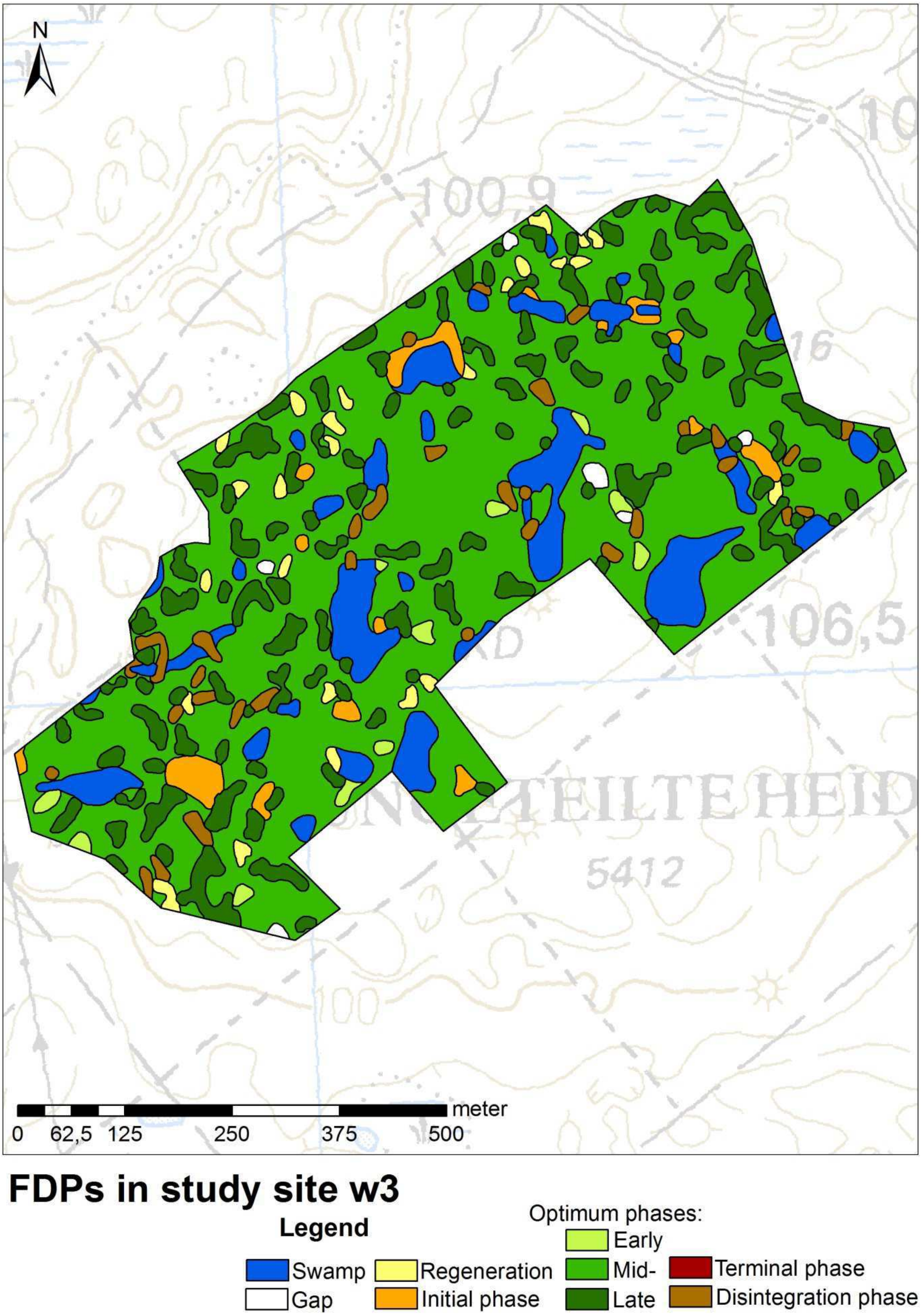


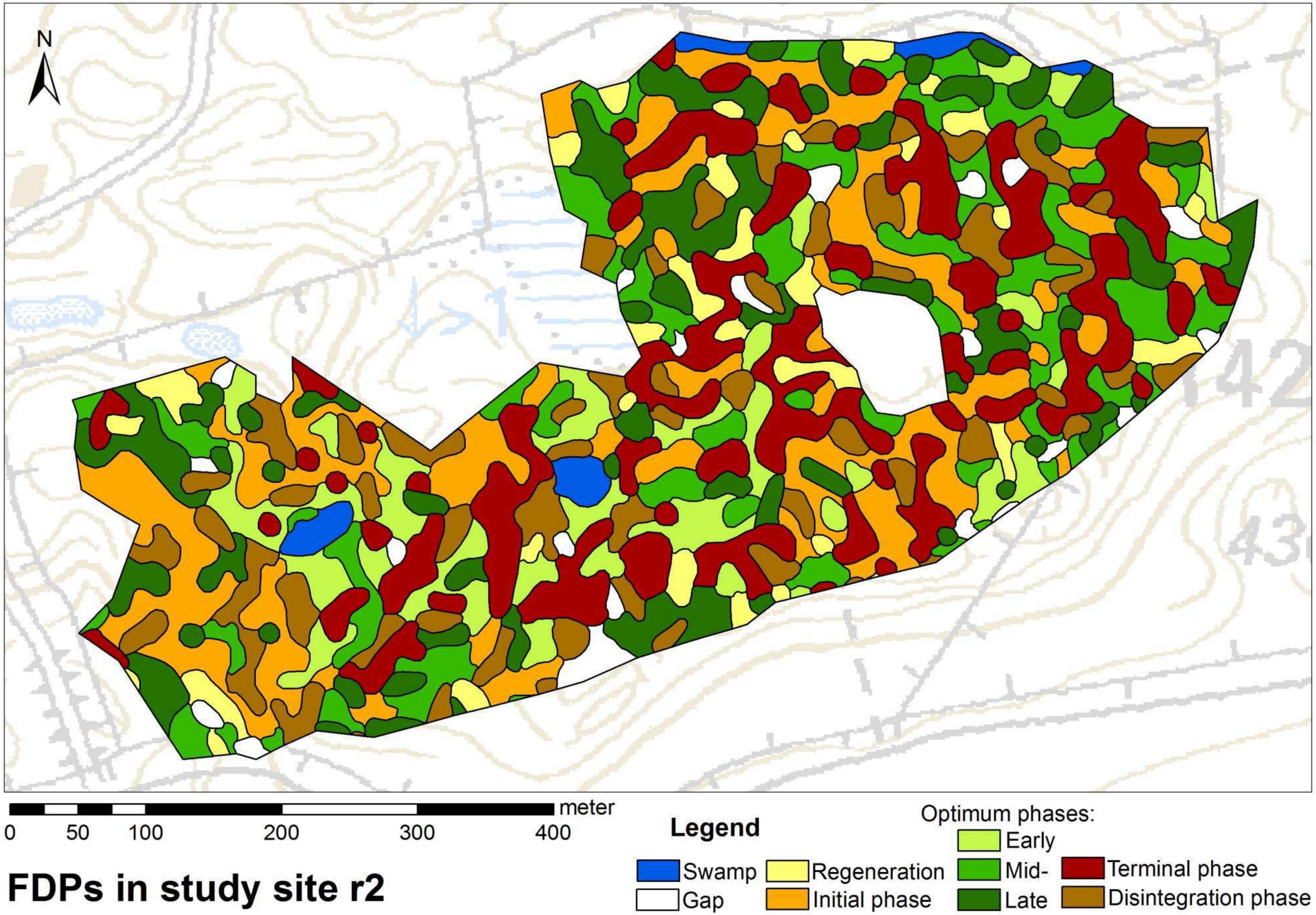
Supplementary Material E Maps of FDPs in 22 lowland beech forest sites.

FDPs in study site r1

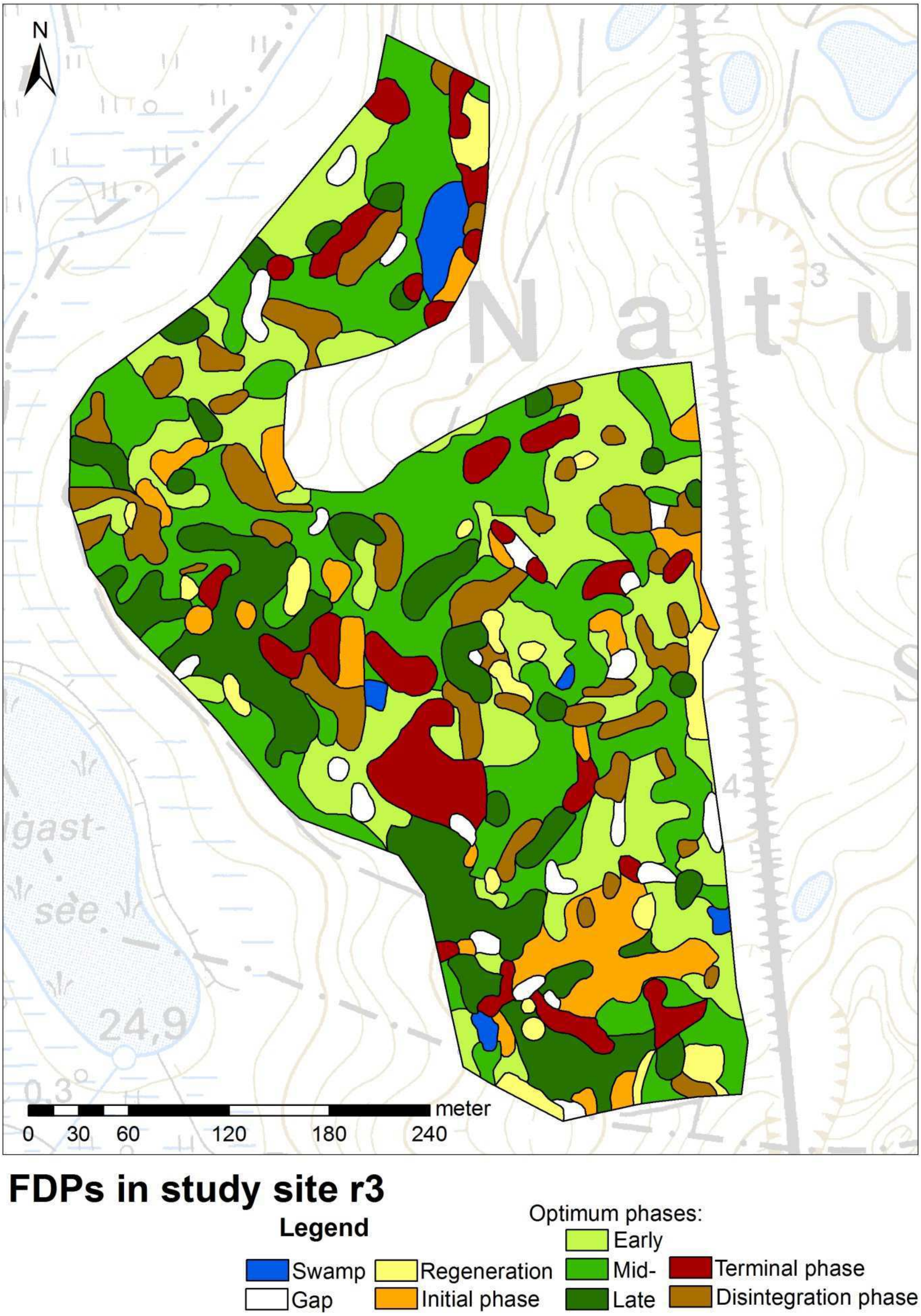
Legend

Swamp
Gap
Regeneration
Initial phase
Optimum phases:
Early
Mid-
Late
Terminal phase
Disintegration phase

Supplementary Material E Maps of FDPs in 22 lowland beech forest sites.



Supplementary Material E Maps of FDPs in 22 lowland beech forest sites.



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